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THE ORIGIN AND DEVELOPMENT OF THE CENTRAL NERVOUS SYSTEM IN LIMAX MAXIMUS.

BY ANNIE P. HENCHMAN.

WITH TEN PLATES.

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No. 7. — *The Origin and Development of the Central Nervous System in Limax maximus.* By ANNIE P. HENCHMAN.[1]

FOR several years the origin of the central nervous system in Mollusks, both as to method and time of appearance, has been a matter of controversy. It has been of especial importance to determine from which of the embryonic layers its parts arise, and to ascertain if its development throws any light on the relations of Mollusks to other important groups of the animal kingdom, particularly Worms.

Since the observations of the earlier writers, down to about 1874, were carried on without the aid of sections, their conclusions do not merit that degree of confidence which is to be accorded those who have availed themselves of this means of study.

Most of the later authors agree that the central nervous system arises from the ectoderm, either by an invagination, or by a simple local thickening which later becomes detached. However, Bobretzky ('76, pp. 162–169), — the first to use sections, — while conceding that in Fusus there are invaginations of the ectoderm to form the sense organs, concludes that the supra-œsophageal and pedal ganglia arise from the mesoderm, and Bütschli ('77, pp. 227, 228) is inclined to believe that the same is true in Paludina vivipara.

Von Jhering ('74, p. 321) claims for Helix, and both Lankester ('74, pp. 382, 383) and Wolfson ('80, pp. 95, 96) for Lymnæus stagnalis, that the central nervous system arises simply from a thickening of the ectoderm.

Fol ('80, p. 664) has since pointed out, however, that Lankester's conclusions are based on an erroneous interpretation of cells ("nuchal cells"), which he believes are not at all nervous in their nature. They are the same cells which Wolfson has called the embryonic brain; but Wolfson's opinion, previously stated, has reference to the definite nervous system, not to this so-called embryonic brain.

Haddon ('82, pp. 368–370) believes that he has seen the rudiments of the cerebral and pedal ganglia of Nudibranchs in the form of thickenings of the ectoderm, and he has made sections of Purpura lapillus and Murex erinaceus which show, as he maintains, that similar rudiments are also formed in them by proliferation from thickenings of the ectoderm.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXI.

Kowalesky ('83, pp. 23–26) shows for Chiton Polii that the lateral and pedal nerve trunks are formed simply as thickenings of the ectoderm.

Rabl ('75, pp. 206–208) maintained that the supra-œsophageal ganglia and the sense organs in Lymnæus, Physa, Ancylus, and Planorbis were formed by an invagination of the ectoderm, and that the pedal ganglia were produced by delamination from the same germinal layer. He has more recently ('83, pp. 57, 58) expressed doubt as to the manner in which the pedal ganglia arise in Bythinia tentaculata, because he has seen them so connected to the ectoderm of the dorsal wall of the foot by means of cells as to indicate that they arise by proliferation from that region.

Sarasin ('82, pp. 45–48), who has also recently studied Bythinia tentaculata, and who is the only author that has hitherto followed the development of the entire nervous system in a Gastropod, contends that the whole of it arises from ectodermic thickenings, without any invagination even for the supra-œsophageal ganglia. He also believes that the pedal ganglia arise from the dorsal wall of the foot.

Fol ('80, pp. 165–169) admits no invagination for the central nervous system in aquatic pulmonates, and he even inclines to the opinion that it may be derived from the mesoderm, which, however, has itself originated from the ectoderm. He considers it an unimportant question, and therefore one which it is useless to discuss, whether the nervous system arises from ectoderm or mesoderm. If the mesoderm were derived from the entoderm, then it would be an important question. He believes that the supra-œsophageal ganglia of land pulmonates (pp. 192–195) originate by invaginations of the ectoderm, while the pedal ganglia arise from the mesoderm of the foot.

The latest investigations are those of Salensky ('86, pp. 655–759) on the development of Vermetus, one of the Prosobranchs. He concludes that the cerebral ganglia are formed by two invaginations of the ectoderm, while the pedal ganglia arise by proliferation from the ventral and lateral walls of the foot on each side of the median depression which runs along its ventral face. These ganglia arise separately, and later become connected with each other by a commissure, and with the cerebral ganglia by connectives, both of which are outgrowths from the ganglia (pp. 694, 695).

Thus we find that, of the authors cited, Bobretzky, Bütschli, and — as far at least as regards the aquatic pulmonates — Fol consider the central nervous system as originating from the mesoderm. Rabl is a little doubtful as to its mesodermic origin in Bythinia. Rabl, Fol, and Salensky are the only investigators who consider any portion of the central nervous system as arising by invagination, and then only in certain Gastropods.[1]

The following observations were made upon embryos of Limax maximus obtained from adults kept in captivity. Under favorable circumstances, they lay abundantly during the latter part of September, and through October and November. After numerous trials, the best method found was to keep about twenty-five or thirty in a large tin pail, the cover being perforated with small holes. Instead of using moss to secure the necessary moisture, the slugs were fed upon lettuce or cabbage; the latter is the better of the two. This food affords at the same time sufficient protection against desiccation, a suitable retreat for the slugs, and a place where they may lay the eggs. It should be changed every other day, — every day if the weather is warm, — and the pail should be washed thoroughly each time. One of the advantages of using a tin vessel is the ease with which it may be kept clean. Cabbage will keep longer than lettuce, and the slugs lay more abundantly when fed upon it. The eggs were generally found in the morning, sometimes at night, in bunches of from thirty to forty. They are more abundant at first than after the slugs have been kept some time in confinement; it is therefore better to obtain at intervals fresh supplies of small numbers of slugs than to procure a larger number at one time. As soon as found, the eggs were removed to a watch-glass containing water; this was placed in a tumbler already about half filled with moss or moistened paper, having a perforated tin cover. The eggs must not be allowed to become dry. For a few days they should be carefully examined under a microscope, every twenty-four hours or oftener, and all those which fail to develop should be removed at once. In the course of a few days these can be readily detected with the naked eye by reason of the greater opacity of the eggs, and the presence of a whitish spot in them due to the disintegration of the embryo.

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[1] The brothers Sarasin, in later researches in Ceylon ('87, pp. 59–69) on a species of very large Helix, find that there are *two* invaginations of the ectoderm on each side of the head to form the cerebral ganglia, and Kowalesky ('83^a) had found several years before that there were in Dentalium two deep invaginations, *one* on each side.

A very large per cent of eggs kept in this way remain in good condition until hatching, which, in a moderately warm room, occurs between the twenty-second and twenty-seventh day.

The best reagents for killing embryos were found to be either chromic acid, 0.33%, or Perenyi's fluid. The chromic material when well stained with alcoholic borax-carmine shows the differentiation of nerve cells and nuclei excellently, but it is more difficult to stain sufficiently chromic material than such as has been preserved in Perenyi's fluid. The latter may be stained with alcoholic borax-carmine or picrocarminate of lithium. Good results for the study of cell division have also been obtained by staining with Czoker's cochineal. The picrocarminate of lithium is particularly valuable in the older stages, because it brings out the nerve fibres, the latter being stained yellow, while the ganglionic cells are colored red.

To obtain the embryos in an uninjured condition, it is advisable, in using the chromic-acid method, to remove only the outer envelope *before* killing. The egg may be held between the thumb and forefinger of the left hand, while with a finely pointed stick, somewhat like a wooden toothpick, the outer membrane is gently punctured; the probe should be run under the membrane a little way, to make a larger opening, and the egg carefully pressed with the thumb and forefinger, whereupon the albumen, containing the embryo and surrounded by the inner membrane, will come out in a perfect condition. This may be dropped at once into water, if several are to be treated together, for it is more convenient to put them all into the chromic acid at the same time. When all have been shelled, they should be put into 0.33% chromic acid for two or three minutes only, simply to kill the embryo without hardening the albumen. Then they should be transferred to a watch-glass of water, to which a few drops of the acid have been added. While in this fluid, the inner membrane may be removed with needles. To accomplish this, it is advisable, in the very young stages, to make as large an opening in the membrane as possible, and then with a needle gently to press the embryo out, even if the albumen adheres to it, for the albumen becomes slightly coagulated in the weak acid, and then can easily be washed off. In the stages from the tenth to the sixteenth day, the large size of the pulsating sacs of both head and foot regions makes it extremely difficult to extract the embryos uninjured; great care must therefore be taken, and *no pressure* used. While employing one of the needles to hold the membrane, the other should be forced through the membrane, which may then be ruptured and turned back over the embryo, being drawn off like the finger of a glove. In the older stages, not much care is necessary, because the embryos bear without injury considerable handling, and there is so little albumen left that their position is not readily changed while the membranes are being removed. When freed from the membranes and as much of the albumen as possible, the embryos are to be returned with a large-mouthed pipette to the chromic acid (0.33%), where they may be left for an hour or two; after washing in running water for two or three hours, they may be carried up to 70% alcohol by adding to the water, drop by drop, 35% alcohol; then 50% alcohol, etc. This dehydration must be made very carefully, to avoid shrinkage. The embryos are extremely delicate, and must be handled with great care through every step of the process.

In using Perenyi's mixture, it is best to free the embryos *while living* from the surrounding membranes and the albumen, removing the inner membrane under clear water. When set free, they should be transferred at once with a pipette into a dish of Perenyi's mixture, where they may remain from *two to three minutes.* They are then to be washed thoroughly in distilled water at least five minutes, put into a 5% aq. sol. of alum for thirty minutes, washed again in water, and finally carried through the grades of alcohol as in the chromic method. It is necessary to remove the embryo while living, because otherwise the albumen becomes in this reagent like a jelly, and cannot be removed without injury to the embryo. Material designed to be sectioned must not be left in alcohol longer than a month, since the albumen in the nutritive sac gradually becomes too hard to be cut, especially if prepared in Perenyi's mixture. The stages from the tenth to the sixteenth day can still be used, even if they have been thus overhardened, by removing the nutritive sac; but in the younger stages this is apt to destroy the embryo, and in the older ones — much of the albumen having been swallowed — its removal is still more certain to have the same effect. Attempts subsequently to soften the albumen by prolonged treatment with weak acetic acid proved to be only partially successful. If the embryos are to be kept at all, they should be left unstained; but the safest way is to carry them through to embedding as soon as possible.

They can be stained whole; but to do this successfully, they must be carried gradually through successively weaker grades of alcohol until a grade corresponding to the stain is reached. It is advisable to make the necessary steps from the stain to the parafine as quickly as possible.

Staining with picrocarminate of lithium has the advantage of saving time, since it acts rapidly,—the older specimens requiring only one or two hours, the younger from half an hour to an hour. A few grains of picric acid may be added to the dehydrating alcohols which follow the stain, in order to prevent the total extraction of the picric acid, and the consequent disappearance of the yellow color from the nerve fibres. If the object is too deeply stained, the differentiation of nerve tissue does not show well; the nerve fibres ought to be yellow, the surrounding nuclei pinkish red with a yellow tinge, and all the other tissue pinkish red. As this and Czoker's cochineal are both aqueous dyes, the chromic material is apt to macerate in them; neither does it stain so well in them as in alcoholic borax-carmine.

The chloroform method of embedding in parafine was used exclusively. When the embryo has been transferred by the well known method to a vial containing chloroform, the vial should be placed uncorked on the water-bath at 55° to 60° C. Pendent spoons in the large cups are not very serviceable, as the least jar sends the objects off, and it is almost impossible to recover them from the bottom of the cup without injury. It is better to have ready on the bath an empty warm glass dish,—a common salt-cellar is very good; also one filled with parafine which melts at about 52° C. The embryos are to be left in the chloroform only as long a time as is necessary for them to sink, and are then to be transferred with the chloroform to the empty glass dish. The transfer is best made by means of a warm pipette, if the embryos are small. Cold soft parafine is then added, a small piece at a time, until the chloroform has so thoroughly evaporated as to leave no trace of its odor. After remaining for fifteen minutes in the soft parafine, the embryo is to be transferred to the "harder" parafine (52° C.), where it should remain from fifteen to thirty minutes. It is important to handle the object with great care, and to carry it through the period of heating as quickly as may be; the latter is necessary, because the embryos are very apt to become brittle if subjected to the heat too long. They should be embedded within an hour or an hour and a half from the time they are first put upon the bath in the chloroform. It is especially dangerous to allow the parafine to harden about the embryo before the latter is finally embedded, because upon the remelting of the parafine the object is almost certain to fall into fragments, owing to its great delicacy.

The embedding, especially for the younger stages, must be done under a lens. It is most convenient to use a dissecting microscope, the stage of which should be kept warm. I have found that parafine which melts between 50° and 52° C. is better for embedding than that which is harder, for the latter is liable in hardening to cause the embryo to crack.

Sections from 10 to 15 μ thick, and in the oldest stages even thicker, are better than very thin ones.

The central nervous system of Limax consists of four pairs of ganglia, — namely, cerebral, pedal, pleural, and visceral, — together with one abdominal ganglion. To these more central ganglia are joined in addition a pair of buccal ganglia, and one mantle or olfactory ganglion.

To summarise briefly in advance my conclusions: The ganglia arise separately. The components of three of the five pairs are joined together later by commissures. Secondarily-produced connectives[1] also serve to join the cerebral ganglia to the pedal, the pleural, and the buccal; the pleural to the pedal and the visceral; and the visceral to the abdominal. The growth of the ganglia is rapid; they are well formed, and in their ultimate positions by the sixteenth day. The principal changes from that time until hatching, eight or nine days later, are increase in size, and modifications of the histological conditions. According to my observations, all the ganglia, with the possible exception of the pleural, are derived directly from the ectoderm, — the cerebral in part from invaginations, the others exclusively by cell proliferation without invagination. The cerebral ganglia are formed by extensive invaginations, one on each side of the head region, just below and behind the base of the ocular tentacles. During the invagination a rapid cell proliferation takes place at the deep end of the invaginated portion of the ectoderm, and also at a region of the ectoderm corresponding to the depression between the labial tentacles and the upper lips. The lateral halves of the cerebral mass arise as two separate structures, — each from a double origin, — which are only secondarily joined. This union is the result of outgrowths from each of the ganglia which, uniting, form the cerebral commissure. The invaginations begin a little later than the proliferation of cells which gives rise to the pedal ganglia, and they remain open as narrow tubes until towards the period of hatching, or even later. In one instance they have been found in this condition as late as eight days after hatching. The cerebral commissure is formed a little earlier than the commissural fibres joining the pedal ganglia. The latter are connected by *two* distinct commissures, the anterior of which is formed earlier than the posterior. The visceral ganglia precede a little in their development the pleural, abdominal, buccal, and mantle ganglia. The buccal ganglia make their appearance at about the same time as the pleural, and undergo almost no change in position.

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[1] In accordance with the usage introduced by Lacaze-Duthiers, the term *commissure* is employed for the nerve fibres joining the components of a pair of ganglia, and *connective* for those between ganglia on the same side of the body.

The nervous system in Limax maximus makes its appearance on the *sixth or seventh day* after the egg is laid. At this time the foot is a conical projection, less than half as long as the diameter of the more or less spherical remaining portion of the embryo, and its pulsating sac is very small. It is a stage which is only slightly older than that represented by Fol in his Planche 17–18, Fig. 7. The ocular tentacles are now distinguishable as small elevations of the head region, near the beginning of the primitive nephridial organs, but the labial tentacles are barely to be made out. The radula sac is a nearly spherical outfolding of the floor of the oral sinus; its fundus is composed of only a single layer of cells, but the part of the sac which is continuous with the wall of the œsophagus is more than a single cell deep; the lumen of the œsophagus is traceable close up to the yolk, where it ends blindly. Both the œsophagus and the radula sac are covered with a continuous layer of somewhat flattened mesodermic cells. The shell gland has the form of a large thin-walled sac containing concretions.

When this condition has been reached, the head region (Plate I. Fig. 2) exhibits no sign of cerebral invaginations, nor have I been able to find regions of cell proliferation or thickenings in the ectoderm which were referable with certainty to the cerebral ganglia.

So far as I have been able to make out, the first contribution to the formation of the pedal ganglia occurs in the form of small clusters of cells, which are still imbedded in the ectoderm of the ventral wall of the foot (Plate I. Fig. 5), from which they are subsequently detached. Each of these clusters has a spheroidal or more ridge-like form, and contains from four to eight cells. The boundaries of the cells are not sharply marked, but the whole cluster is limited by a definite outline separating it from the rest of the ectoderm. Each cell contains a nucleus, which is large, but less deeply stained than those of the ectoderm, and each nucleus has a large nucleolus, which is very deeply stained (Plate I. Fig. 1).

The region in which this proliferation takes place is definitely located, for it lies in the same transverse plane in which the otocysts (Plate I. Figs. 3, 4) are situated, and it is found at a region in that plane intermediate between the lateral border of the foot and its middle line, but considerably nearer the former. The proliferating cells project into the cavity of the foot, and ultimately are separated from the ectoderm.

Although cells which closely resemble these are found in groups in other parts of the body wall, their nuclei do not become as large as those of the cells destined to form the ganglia. Moreover, the proliferations are constant and most abundant in the regions where the different ganglia of the nervous system take their origin. Besides, in these cases there is generally a sinking in of the surface of the ectoderm in the same region.

Somewhat later than at the stage described, usually on the *seventh day*, the external conditions still remain nearly the same, the ocular tentacles being perhaps a little more prominent, and the concretions in the shell gland more numerous.

The cells of the primitive entoderm, which surround the yolk, form a striking feature of the condition at this stage. These entoderm cells are very large, vacuolated, and only slightly stainable. They contain large ovoid nuclei, which are crowded to one margin of the cells by the nutritive contents accumulated in the cells. Each nucleus contains one large deeply stained nucleolus, and a network of chromatic substance (Plate I. Fig. 2). The ectoderm, except over the nutritive sac, consists of elongated cells, whose nuclei are so arranged as to give the appearance of two or more layers. The ganglionic cells at this time closely resemble the mesodermic cells, and this makes it difficult to distinguish between the two (Plate I. Fig. 7).

The internal ends of the primitive nephridial organs are situated one on each side of the head, immediately above and back of the ocular tentacles. These organs pass at first forwards and upwards, then in an arch backwards over the nutritive sac, and finally downward and forward. Their external openings are far back in the lateral walls of the body, behind the head region. The organs are readily distinguished in sections by their large slightly stained cells, which are arranged in a single layer around an oval lumen. The large nuclei contain each a single deeply stained nucleolus (Plate I. Figs. 2 and 6). The primitive entoderm and the nephridial organs retain this histological condition throughout the embryonic stages.

The cerebral invaginations at first appear as shallow depressions in the ectoderm at the base of the ocular tentacles, at a point immediately below the nephridial organs. At the same time that the infolding takes place, cells, whose nuclei are larger than those of the mesodermic cells, are being proliferated from the deep surface of the invaginating portion of the ectoderm (Plate I. Fig. 6).

In the region of the ventral wall of the foot referred to in the stage previously described, there are in the ectoderm of each side of the body two groups of ganglionic cells (*prf. pd.*, Plate I. Fig. 7), one behind the other. These cells project into the cavity of the foot, and reach nearly to another small group of cells situated not far from the ventral wall. The cells of the latter group (there is one group on each side of the body) have nuclei similar to those of the cells still connected with the ectoderm. Each group lies in the position subsequently occupied by the pedal ganglion of its side of the body, and is undoubtedly the beginning of that ganglion, for the cells in the ventral wall of the foot continue to be proliferated during several days, and are found in some individuals to be in direct continuity with the ganglia after the latter have attained considerable size. In the individuals shown in Figures 7 and 9 (Plate I.), the right otocyst (Fig. 7) is seen as a closed vesicle, which is not yet wholly detached from the ectoderm. The otocysts undoubtedly vary in regard to the time of their detachment, as will be seen by a glance at the left otocyst of the same individual, which has entirely lost its connection with the ectoderm (Fig. 9).

All the other ganglia, with the exception of the one near the olfactory organ and the buccal ganglia, arise by cell proliferation from ectoderm which lies between the foot and the head region, either at or a little above the posterior angle formed by the body wall with the dorsal surface of the foot, or along a depression which runs forward from this point. This angle marks the posterior limit of a furrow which passes obliquely forward and downward, partially separating the head and visceral mass from the foot. This depression will be designated as the *pleural groove.* Of the remaining ganglia, only the visceral have begun to be formed at this time. The cells destined to form these ganglia are situated immediately above the angle produced by the pleural groove (Plate I. Figs. 8 and 9). Some of those of the left ganglion are wholly detached from the ectoderm, but those of the right (Fig. 7) are still continuous with the ectoderm, though projecting into the body cavity. The cells have large, round, faintly stainable nuclei, each containing one large nucleolus, which takes a deep stain.

Twenty-four hours later, about the *eighth day*, the pulsating sac of the foot has become still larger, and the oral sinus has extended backward and downward as a very narrow tubular passage, — the œsophagus, — which follows the surface of the nutritive sac for some distance, and subsequently opens into it. The peculiar ciliated cells of great size and spongy appearance, which occupy a linear tract along the middle of the roof of the mouth and œsophagus, are at this time very prominent (Plate I. Fig. 2, *loph. cil.*). These cells form what Fol ('80, pp. 190, 191) has called the "ciliated ridge." They persist until after the completion of the nervous system. The ingrowth of the ectoderm to form the rectum is now composed of a compact group of small cells, which shows a small lumen in its central portion, but is still closed at both ends.

The cerebral ganglia remain in nearly the same condition as that last described. About twelve hours later, between the eighth and ninth days, the two cerebral invaginations have become deeper, and the two groups of cells which form the main portions of the corresponding ganglia contain a greater number of cells. (Plate II. Fig. 15.)

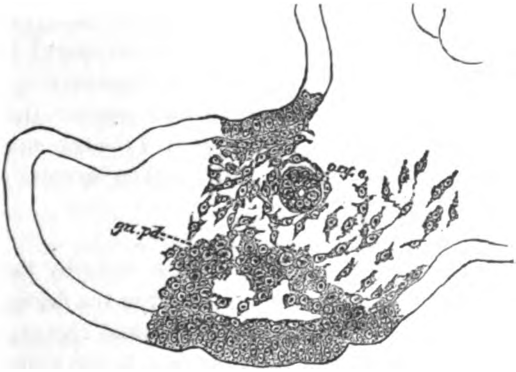

FIGURE A. — The right face of a section parallel to the sagittal plane from an embryo of the *ninth day* × 220.

gn. pd. Pedal ganglion *o cy. s.* Left otocyst.

The pedal ganglia are also now composed of many more cells than in the previous stage. Each ganglion is usually pear-shaped, and tapers towards the posterior end of the foot. They both continue to receive accessions from the ectoderm (Figure A), and at the same time are rapidly increasing in size by division of the cells already in position. The nuclei are larger and more easily distinguished than in the previous stage from those of the mesodermic cells, the latter being more spindle-shaped than before. The cells of the mesoderm form a continuous layer along the inner surface of the ectoderm, except where cell proliferation is taking place (Figure A).

As yet nothing is to be seen of the pleural ganglia.

The visceral ganglia have increased in size (Plate I. Figs. 10, 11, 12); they are still connected with the ectoderm (Figs. 10, 12), although a few cells with large nuclei have become detached from it (Fig. 11). The ganglion and the otocyst of the same side of the body lie in nearly the same sagittal plane. Each ganglion is situated just above the angle caused by the pleural groove. The right visceral ganglion (Fig. 10) is somewhat farther forward and more dorsal than the left (Figs. 11, 12).

About in the median plane of the body, and above the angle made by the pleural groove, are the cells which form the abdominal ganglion (Plate I. Fig. 13). The greater part of them are still embedded in the ectoderm. Although in some regions they project into the body cavity, they are nowhere wholly separated from the ectoderm. The abdominal ganglion seems to be at first more intimately connected with the left visceral ganglion than with the right, but a connective is formed with both of them a little later, and the abdominal ganglion thus appears to occupy the place of a direct commissure between the two visceral ganglia. As development proceeds, the abdominal ganglion becomes closely fused with both the visceral ganglia.

Quite an advance in external conditions is made by the *ninth day*. But individuals of the same age vary so much in the degree of development attained by both their external and internal organs, that the age assigned can be taken only as an approximation to the average condition at the time indicated.

The tentacles appear as protuberances, the labial tentacles being much smaller than the ocular; the shell gland contains more concretions, the mantle is larger and bends backward over the dorsal surface of the foot. The radula sac makes its appearance and extends backward into the foot, where it ends blindly immediately back of the pedal ganglia. In transverse sections it appears flattened dorso-ventrally; its lumen is oval, and the ectoderm lining it is more than one cell deep.

The cerebral invaginations (Plate II. Figs. 15, 19, Plate III. Figs. 25, 26) are much deeper, the infolding ectoderm is greatly thickened, and the incipient ganglia receive accessions from ectodermic depressions between the rudiments of the upper lips and the labial tentacles (Plate II. Fig. 21). The cerebral commissure (Fig. 21) is also being formed, the cells of the median portion of each ganglion growing out to meet the corresponding cells from the opposite ganglion. The commissure at this stage is composed of a small number of cells, which are very much elongated. The fibres resulting from their elongation already make a continuous bridge from one ganglion to the other.

The pedal ganglia (Plate II. Fig. 20, Plate III. Fig. 27, Plate V. Fig. 60) consist of two small groups of cells, situated about midway between the sole of the foot and the posterior end of the radula sac. They are a little below and behind the pleural groove and the otocysts, and they are farther from each other than from the lateral wall of the foot. There is a slight indication of a commissure (Plate III. Fig. 27) joining their anterior portions to each other. The commissure is formed in the same manner as the cerebral commissure, the individual cells composing it being spindle-shaped, with their nuclei somewhat elongated in the direction of the fibres.

The otocysts (Plate II. Fig. 20, Plate III. Fig. 27, Plate V. Fig. 60) are on a level with the lower margin of the radula sac, and are nearer the pedal ganglia than in the preceding stage.

On each side of the body above the pleural groove is a group of a few cells, which are in all probability the first indications of the pleural ganglia (Plate II. Figs. 14 and 20). The centre of each cluster is seen on cross sections (Fig. 20) to be nearly on a level with the lumen of the radula sac. The cells at this stage are very small, and so loosely associated that it is difficult to distinguish them from mesodermic cells. I have not satisfactory evidence of their origin directly from the ectoderm, for, although I have found them at times very near to the ectoderm (Fig. 20), I have never found them at any stage continuous with it. On the other hand, I have not seen conditions which would warrant the conclusion that the ganglia were the result of outgrowths from either of the pre-existing ganglia.

A little before the ninth day the cells detached from the ectoderm to form the visceral ganglia (Plate II. Figs. 17, 18) increase rapidly in size, and the diameter of their nuclei often becomes four or five times as great as that of the ectodermic nuclei. The ganglia consist of elongated groups of such cells, still attached to the ectoderm above the pleural groove (Figs. 16, 18). The want of symmetry in the positions of the right and left ganglia is more conspicuous than in the preceding stage, the ganglion of the right side being considerably more dorsal and farther back than that of the left side (Plate II. Fig. 23, Plate V. Fig. 60). Owing to the infolding of the ectoderm on the right side of the body to form the respiratory chamber (Plate II. Figs. 16, 24), the region from which the ganglionic cells arise is now located on the ventral and median walls of the infolding. The ganglia have also grown forward, and lie between the nephridial organs and the nutritive sac (Plate II. Fig. 23). In an individual cut crosswise, the posterior portion of the ganglia is found to be two or three sections back of the otocysts. Both the ganglia may be traced through five or six sections.

A little behind the visceral ganglia, and to the left of the median plane of the body, are the prominent cells of the abdominal ganglion (Plate II. Figs. 24, *ab.*).

All of these ganglia still consist of groups of loosely associated cells. Later they become more compact, and are surrounded by connective-tissue cells.

The buccal ganglia (Plate II. Fig. 22), first seen with certainty at this stage, arise, one on each side of the radula sac, at the angle between it and the œsophagus. It is to be seen from cross sections that the cell proliferations from which they spring take place from the dorsal wall of the neck of the sac, where its lumen begins to be separated from that of the œsophagus. This is also their permanent position; they are later joined together by a commissure, which results from outgrowths of the cells composing the two ganglia.

On the *tenth day* the external appearance of the embryo remains nearly the same as before, with the exception that there is an increase in the size of the embryo, and especially of its pulsating sacs. The sac of the radula has become more elongated, and the anal opening (Plate III. Fig. 31, *an.*) is formed.

The cerebral invaginations still appear, in sections parallel to the sagittal plane (Plate III. Figs. 28 and 29), as shallow depressions. The number of cells in each ganglionic group (Plate IV. Fig. 58, Plate V. Fig. 63) has increased perceptibly. At the same time the groups have extended backward, and show indications of the cerebro-pleural connectives. In specimens cut in the sagittal plane, the cerebral commissure cut crosswise may be seen above the oral opening (Plate III. Fig. 30).

The pedal ganglia (Plate IV. Figs. 54, 58, Plate V. Fig. 63) have increased in size. Their anterior borders now reach as far forward as the plane of the pleural groove, and they extend backward into the foot much farther than before. In cross sections (Plate IV. Fig. 54) they appear as rounded groups of cells, which are far apart and not yet very compact; they still continue to receive accessions by the proliferation of ectodermic cells from the walls of the foot (Plate IV. Fig. 57, 58, *prf.*). The first decided evidence of a pedal commissure makes its appearance during this stage. It consists (Fig. 54) of a few very much elongated nerve cells, which stretch across from one ganglion to the other a little posterior to the region of the otocysts. The commissure may be traced on about half a dozen successive sections, or for a distance of some 50 or 60 μ. From its position it evidently is the beginning of the *anterior* commissure. The thickness (10 μ) of a single section contains only three or four cells, the nuclei of which have the chromatic substance so concentrated into a single nucleolus as to make the nuclei appear clearer than those of the surrounding connective-tissue cells. There is at present no trace of a posterior commissure. The otocysts are now nearer the ganglia (Plate IV. Fig. 58, Plate V. Fig. 63) than at any previous stage.

The pleural ganglia (Plate V. Fig. 63) are still inconspicuous, being composed of only a few scattered cells, which lie nearly dorsal to the otocysts, about midway between the visceral and the cerebral ganglia of the same side of the body. Many of the cells are elongated in the direction of the ganglia between which they are located, and appear to form the beginning of a connective between them.

The visceral ganglia (Plate IV. Figs. 58 and 59, *vsc.*) are still connected with the ectoderm, but project more prominently from the wall of the body, and extend forward more than before. The right (Plate IV. Fig. 59) is larger, and still lies more dorsal, than the left (Plate V. Fig. 63). The cells which compose the ganglia are numerous and large, and the nuclei of those which form the centre of the ganglion are conspicuously larger than those at the periphery. In cross sections of a stage possibly a little less developed than the one last described, the ganglia (Plate IV. Figs. 53, 56, 57, 55) lie, one on each side of the body, immediately above the pleural groove, a little below and inside the external orifices of the primitive nephridial organs. On the right side of the body the ectoderm which constitutes the anterior wall of the infolding to form the mantle chamber is seen in sagittal sections (Plate IV. Fig. 58) to be much thicker in the region adjoining the pleural groove than in that which forms the deeper portion of the infolding. The transition from the thick to the thin ectoderm is very abrupt, and is marked by a pocket-like depression. The right visceral ganglion is situated at the side and in front of this depression. Some of the cells in the anterior portion of this ganglion (Plate IV. Fig. 56) are traceable toward the median plane of the body. The left visceral ganglion

(Figs. 56, 57) is not yet as large as the right, and it consists of fewer cells.

The position of the connective between the visceral and pleural ganglia (Plate V. Fig. 63) is indicated by the presence of spindle-shaped cells with fibrous projections. The connective is at this time long, and the cells and fibres composing it are only joined to one another loosely.

As the abdominal ganglion increases in size, it extends more toward the right side of the body (Plate V. Fig. 61), and the connective between it and the right visceral ganglion, which is hardly perceptible at this stage, is much shorter than that to the left visceral ganglion.

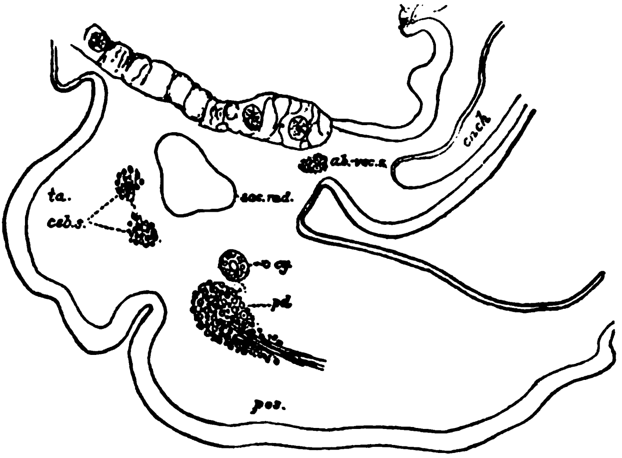

Figure B. — The left face of a section parallel to the sagittal plane from an embryo of the *eleventh day.* × 73.

ab.-vsc. s.	Left abdominal-visceral connective.	*pd.*	Pedal ganglion.
ceb. s.	Left cerebral ganglion.	*pes.*	Foot.
cnch.	Shell gland.	*sac. rad.*	Radula sac.
o cy.	Otocyst.	*ta.*	Ocular tentacle.

The buccal ganglia remain in the same condition as in the preceding stage (Plate II. Fig. 22).

By the *eleventh day* the embryo has increased greatly in size (Figure B); the tentacles are prominent, and the pulsating sac of the foot is very large. A narrow slit-like infolding of the ectoderm (compare Plate VIII. Fig. 101, *gl. pd.*) has arisen in the median plane of the body at the anterior end of the foot, into which it extends backward a short distance. It is the beginning of the foot gland. The salivary glands also make their appearance during this stage as a pair of evaginations of the lateral walls of the œsophagus, immediately above its communication with the radula sac, and a little in front of the buccal ganglia (Plate VI. Figs. 77–80).

The cerebral invaginations still open broadly at the sides of the head (Plate III. Figs. 32–34, and Figure C). They are, however, quite deep, and in a series of sagittal sections the depression becomes deeper and deeper as one approaches the median plane, and at the same time the orifice which leads to the depression becomes narrower and narrower, until it is almost slit-like (Figs. 32–40). The deep ends of the invagination are turned a little towards the median plane. These invaginated portions of the brain are composed of small, closely packed cells, whose nuclei stain deeply. The proliferated portions of the cerebral ganglia, which are deeper than the sacs (Plate V. Fig. 64, Plate VI. Figs. 70, 71), extend toward each other in the median plane, and backward and downward toward the pedal ganglia (Fig. 71). They have now become differentiated into a fibrous central part (Fig. 71), in which

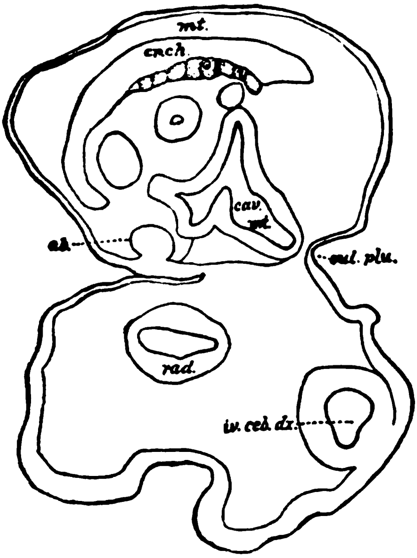

Figure C. — The posterior face of a transverse section from an embryo of the *eleventh day*. × 73.

ab.	Abdominal ganglion.	*mt.*	Mantle.
cav. mt.	Mantle cavity	*rad.*	Radula sac.
cnch.	Shell gland.	*sul. plu.*	Pleural groove.
iv. ceb. dx.	Right cerebral invagination.		

are lodged the larger scattered cells with their very large nuclei, and a peripheral part, where the cells are crowded together and the nuclei are smaller (Fig. 70). They are loosely enveloped by spindle-shaped, very much elongated, connective-tissue cells (Fig. 71). Immediately above the oral cavity is the cerebral commissure (Plate VI. Fig. 80ᵃ). It can be traced from one side of the brain to the other, and its cross section appears as a very small round patch of fibrous substance, surrounded on the dorsal side by a layer of flat cells.

The cerebro-pedal connectives are indicated (Fig. 71) by a few cells extending from the ventral-posterior ends of the cerebral ganglia to the anterior ends of the pedal, a little in front of the cerebro-pleural connectives (Fig. 70). The latter extend from the posterior ends of the cerebral to the anterior ends of the pleural ganglia, thus diverging somewhat from the cerebro-pedal connectives. There are found in the ganglia many cells which are in different stages of division. It is owing to this cell division that the ganglia increase rapidly in size, especially after they are wholly cut off from the ectoderm; cells in the commissures and connectives are also found in process of dividing in planes perpendicular to the direction of their fibres.

The principal change in the pedal ganglia (Plate VI. Fig. 71) is due to an increase in size, particularly in the antero-posterior direction. The central portion of these ganglia has the same fibrous appearance as that described for the cerebral ganglia, and the pedal nerves can be traced for a considerable distance toward the tip of the foot (compare Figure E, page 191). The anterior commissure (Plate III. Fig. 44, Plate VI. Fig. 74) is now somewhat shorter than in the previous stage, and consists of a greater number of cells. Cell proliferation is still taking place from the ectoderm of the ventral wall of the foot (Plate VI. Fig. 71), and the ganglia continue to receive accessions from these sources. More highly magnified views of the regions of proliferation are given in Plate VI. Figs. 72 and 73.

The pleural ganglia (Plate VI. Fig. 70) are now easily recognized. Each ganglion is formed of a triangular group of cells, occupying a position immediately above and anterior to that part of the pleural groove which is nearest to the otocyst. The cells composing the ganglion are fewer than those of any of the other pairs of ganglia, but resemble them in their histological conditions; they are only loosely connected, and their fibres are elongated in the directions of the three connectives. At this stage the ganglia are not closely enveloped in connective tissue.

The pleuro-visceral connectives are well developed, especially the left one (Fig. 70); the right one is much longer and more attenuated, since the right visceral ganglion is farther from the pleural than the left visceral. The ganglia are most distinctly seen in specimens cut in a sagittal direction.

The visceral ganglia (Plate V. Figs. 67–69, Plate VI. Fig. 70) are much larger and more elongated in the direction of the pleural ganglia — i. e. downward, forward, and outward — than they were during the previous stage. They are still connected with the ectoderm at their posterior dorsal ends, while the opposite ends are much drawn out toward the pleural ganglia (Figs. 69, 70). The right visceral ganglion (Figs. 67–69) is larger than the left, and its longest axis has a dorso-ventral direction (Fig. 68). The fibrous prolongations continue into the pleuro-visceral connectives (Fig. 71).

The abdominal ganglion (Plate III. Figs. 43, 44, 46, 47, Plate VI. Figs. 75, 76), although still connected with the ectoderm, is also larger, and projects more into the body cavity than on the tenth day. A large portion of it still lies to the left of the median plane of the body (Plate VI. Figs. 75, 76), and the connective to the left visceral is well developed (Plate III. Figs. 41, 42, Plate V. Fig. 68); that to the right is less complete (Plate III. Figs. 45, 51).

The buccal ganglia (Plate V. Fig. 62, Plate VI. Fig. 77) are now very distinct; the dorsal wall of the radula sac still contributes to their increase in size.

Cell proliferation takes place from the ectoderm bordering the entrance to the respiratory cavity. A few cells, which probably form the olfactory ganglion, are seen at this stage to be separating from the ectoderm in this region.

For the next twenty-four to thirty-six hours (*twelfth and thirteenth days*) the external appearance of the embryo remains nearly the same as on the eleventh day. In the living embryo the larval heart may be seen pulsating, and the foot gland extends somewhat farther towards the posterior extremity of the foot.

The cerebral invaginations appear simply as long narrow sacs filled with a coagulated substance; the inner ends of these sacs have grown upward as well as backward (Plate VII. Fig. 94). The proliferated portions of the cerebral ganglia (Fig. 94) are much larger, and have now assumed more nearly their ultimate positions (Plate III. Figs. 48, 49; Plate VII. Figs. 81, 82, 94). The central portion of each has become more fibrous (Fig. 81).

The connectives, both to the pedal (Plate VII. Fig. 81) and to the pleural ganglia (Plate III. Fig. 48), are well developed, and are both thicker and shorter than in the stage last described.

The pedal ganglia do not differ materially from the condition described for the eleventh day. The anterior end has increased in diameter, and has grown a little farther forward (Plate III. Fig. 50, Plate VII. Figs. 81, 91).

Both commissures are now present; the anterior (Fig. 92) is a little behind the otocysts (compare Fig. 92 with Fig. 91), and the posterior (Fig. 90) is directly above the blind end of the foot gland, and about 0.2 mm. back of the anterior commissure.

The pleural ganglia (Plate III. Fig. 48, Plate VII. Figs. 82, 83, 88) are very near the cerebral ganglia, as may readily be seen in sagittal sections (Figs. 48, 82), and the fibrous connectives to the other ganglia are plainly to be distinguished. The ganglia have become more compact and rounded, and occupy a position nearer the middle plane of the body (Figs. 86, 88).

The visceral ganglia (Plate III. Fig. 49; Plate VII. Figs. 83, 84, 86–89), although they have increased greatly in size, are still connected with the ectoderm which forms the anterior wall of the mantle chamber (Figs. 88, 89).

They have also moved inward and forward. The right ganglion (Figs. 49, 83, 87–89) is especially well developed, and much farther forward than in the previous stage. Its axis is prolonged into a nerve, which runs upward and backward, probably to the olfactory ganglion (Figs. 84, 87).

The connective from the right visceral to the abdominal ganglion passes backward and inward (Plate VII. Figs. 83, 84). Where the connective leaves the visceral ganglion (Fig. 83), the nuclei of the ganglionic cells are very large, and the fibres are very much elongated in the direction of the connective.

In specimens cut crosswise the nerve which forms the dorsal prolongation of the axis of the visceral ganglion is found far forward, in front of the anterior face of the abdominal ganglion; it passes upward and inward (Plate VII. Figs. 87, 88), and is connected with the ectoderm that forms the wall of the small infolding from the respiratory cavity (Fig. 88) referred to in the account of the tenth day. This region is at the same level as that with which the abdominal ganglion is connected farther back (Plate VII. Fig. 93). The ectodermic cells to which this nerve is distributed form the lining to an irregular infolding from the median face of the respiratory cavity, and the lumen of the infolding connects by a narrow orifice with the respiratory chamber (Fig. 88, *cav. mt.*). I believe this is the organ first described by Lacaze-Duthiers.

A little farther forward the right visceral ganglion sends to the right side of the body a nerve (Plate VII. Fig. 89 *n.*), which passes between the wall of the mantle chamber and the primitive sexual duct, probably to be distributed to the right half of the mantle.

At this time the greater portion of the abdominal ganglion (Plate VII. Figs. 81, 82, 85, 86, 93) lies on the right side of the median plane, although it is joined to the left visceral by a large and prominent connective (Plate III. Figs. 50, 52, Plate V. Figs. 65, 66, Plate VII. Fig. 93). Since the visceral ganglia have grown inward and forward, the abdominal ganglion now occupies a position considerably posterior to them (Plate VII. Figs. 83, 86); it lies above the right side of the radula sac. Its posterior dorsal margin is still continuous with the ectoderm of the wall of the respiratory cavity (Fig. 93), but farther forward it is entirely separated from the ectoderm (Fig. 85), and is surrounded by a layer of connective-tissue cells. All the other ganglia are similarly enveloped in connective tissue except where they are continuous with the ectoderm.

The connective to the left visceral ganglion (Plate VII. Fig. 93) passes downward, forward, and outward to the left side above the radula sac.

The buccal ganglia (Plate VII. Fig. 81) are larger than on the tenth day, but are closely applied, as before, to the walls of the radula sac. Their commissure (Plate V. Fig. 65) is embraced in the angle between the œsophagus and the neck of the radula sac, and in sagittal sections presents a circular outline.

On the *fourteenth day* the upper lips as well as both pairs of tentacles are very prominent, and the foot gland has grown backward still farther into the foot (Plate VIII. Fig. 102). The salivary glands have now become elongated into tubular organs with a circular lumen and thick walls consisting of a single layer of epithelial cells (Plate VIII. Fig. 106). They reach a little farther back than the buccal commissure; in passing forward they lie on either side of the œsophagus, about on a level with its lower border. They pass along the dorsal side of the buccal ganglia, and then suddenly bend downward to open into the œsophagus.

The cerebral invaginations (Plate VIII. Fig. 96) present the same general appearance as in the stage last described, but the lumen of the sacs is smaller (Plate X. Figs. 121, 126); in cross sections (Fig. D) it appears oval. The walls are thick, being composed of spindle-shaped cells arranged perpendicularly to the axis of the sac and so crowded that the nuclei are three or four deep.

The proliferated portion of the cerebral ganglia (Plate IX. Fig. 114) retains its pear-shaped condition, but is shorter and thicker. A ventral and median portion of each ganglion forms a small rounded lobe (Figure E). These lobes are near the bases of the upper lips, and in sagittal sections appear almost completely separated from the larger part of the ganglia by ingrowths of connective tissue. It is from these lobes that the pedal connectives arise. The connectives to the pleural ganglia emerge from

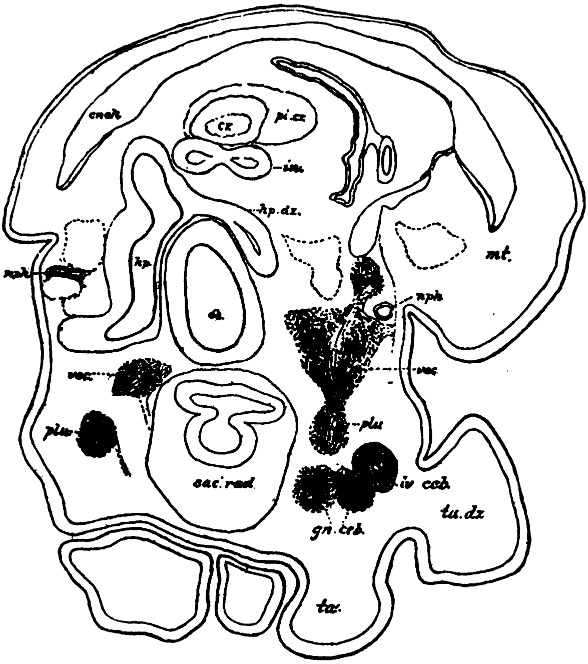

Figure D. — Posterior face of a transverse section from an embryo of the *fourteenth day*. × 190.

cnch.	Shell gland.	*nph.*	Nephridial organ.
cr.	Heart.	*œ.*	Œsophagus.
gn. ceb.	Cerebral ganglion.	*pi. cr.*	Pericardium.
hp.	Liver.	*plu.*	Pleural ganglion.
hp. dx.	Right lobe of liver.	*sac. rad.*	Radula sac.
in.	Intestine.	*ta. dx.*	Right ocular tentacle.
iv. ceb.	Cerebral invagination.	*ta'.*	Labial tentacle.
mt.	Mantle.	*vsc.*	Visceral ganglion.

the larger portion of the ganglion; they are thicker and shorter than the cerebro-pedal connectives, from which they are separated by only a narrow space.

The cerebral commissure is much shorter than before (Plate X. Fig. 126), but it has not increased much in thickness (Plate VIII. Fig. 101). In sagittal sections it is seen to be composed of a central portion made up of nerve fibres cut crosswise and a peripheral layer of nuclei; but the nuclei are wanting on the face of the commissure which is in contact with the dorsal wall of the œsophagus.

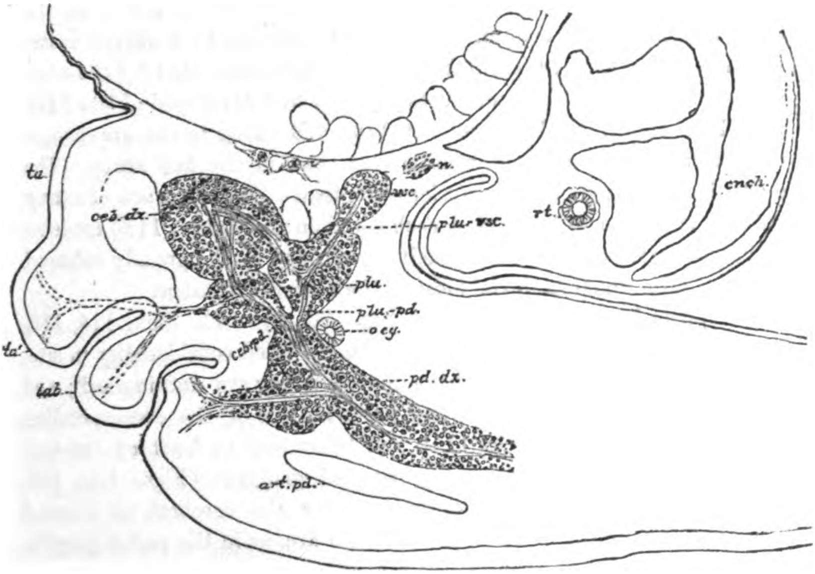

FIGURE E. — The left surface of a section parallel to the sagittal plane from an embryo of the *fourteenth day*. × 73

art. pd	Pedal artery.	*plu -pd.*	Pleuro-pedal connective.
ceb. dx.	Right cerebral ganglion.	*plu.-vsc*	Pleuro-visceral connective.
ceb.-pd.	Cerebro-pedal connective.	*pd. dx.*	Right pedal ganglion.
cnch.	Shell gland.	*rt.*	Rectum.
lab.	Lip.	*ta.*	Ocular tentacle.
n.	Nerve	*ta'.*	Labial tentacle
o cy.	Otocyst.	*vsc.*	Visceral ganglion.
plu.	Pleural ganglion.		

The pedal ganglia (Plate VIII. Figs. 97–100, Plate IX. Figs. 114, 118, 119) lie between the radula sac, which is above, and the foot gland which is below them. They are nearer together than on the twelfth day, and their anterior ends are more rounded (Fig. 114). Their posterior ends are elongated and continued as two large nerves far back into the foot. In specimens cut crosswise these nerves appear as rounded patches of fibres, situated one on each side of the body, above the plane of the foot gland and about midway between it and the lateral walls of the foot. Each is surrounded by a layer of connective-tissue cells. As one approaches the pedal ganglia in passing from behind forward, the nerves increase in size and lie nearer to each other. In the region of the posterior commissure (Plate IX. Fig. 119) the ganglia are nearly as broad as in the region of the anterior commissure (Fig. 118), but they are not much more than half as thick in the dorso-ventral direction. In front of the posterior commissure they are separated by a narrow space, which is wider behind than in front, where it is terminated by the anterior commissure. The commissures are both well developed (Plate VIII. Figs. 101, 102, Plate IX. Figs. 118, 119), and owing to the approximation of the ganglia have become shorter than in the last stage. The nuclei in the region of the posterior commissure (Fig. 119) are of nearly uniform size; but in front of it each ganglion (Figs. 114, 118) contains a fibrous central portion immediately surrounded by the greatly enlarged nuclei of cells which form the most of the fibrous substance.

The pleural ganglia (Plate VIII. Fig. 106, Plate IX. Figs. 114, 116, Plate X. Figs. 123, 125, and Fig. E) have increased considerably in size, and are more compact. They have moved downward and inward; and each now lies in contact with the posterior face of the corresponding cerebral mass (Plate IX. Fig. 114), and below and in front of the ventral portion of the corresponding visceral ganglion (Figs. 106, 123, 125). They are much smaller than either the cerebral or visceral ganglia. The nuclei of their central cells are, as in the pedal ganglia, much enlarged.

The visceral ganglia (Plate VII. Fig. 95, Plate IX. Fig. 114, Plate X. Figs. 123, 125) are now entirely detached from the ectoderm, and have moved downward, forward, and inward.

The left ganglion (Plate VIII. Fig. 106, Plate X. Fig. 125) is smaller than the right, and more closely connected with the left pleural (Fig. 125) than in the previous stage. Its dorsal surface is slightly above the level of the dorsal wall of the radula sac, and its connective with the abdominal ganglion (Plate VIII. Fig. 104) is much broader than before. The right visceral ganglion (Plate VII. Fig. 95, Plate VIII. Figs. 102 and 106, Plate IX. Fig. 114, Plate X. Fig. 123) is much larger than in the last stage; it is also closely connected with the right pleural ganglion (Fig. 123). It extends dorsally much farther than the left visceral, and also nearer to the median plane (Plate VII. Fig. 95, Plate VIII. Fig. 102, Plate IX. Fig. 120). It is in contact with the lower surface of the right end of the abdominal ganglion (Plate VII. Fig. 95).

The abdominal ganglion (Plate VII. Fig. 95, Plate VIII. Figs. 101, 102, 104, Plate IX. Figs. 115–117, Plate X. Fig. 123) is entirely unconnected with the ectoderm, and has moved forward, so that there is a considerable space between it and the pleural groove, but its posterior face extends farther back than that of the right visceral ganglion (Plate VIII. Fig. 102). The greater portion of the ganglion is now situated on the right side of the body, immediately above and to the right of the radula sac (Plate VIII. Fig. 104, Plate IX. Figs. 115–117). It is elongated, and its chief axis is directed obliquely across the body, the right end being considerably higher and a little farther back than the left end. In passing downward and forward to the left side of the body, it lies between the œsophagus and the posterior part of the radula sac. Its left end is prolonged into a connective, which passes forward and outward to join the left visceral ganglion (Plate VIII. Fig. 104, Plate X. Fig. 123). A large nerve, which passes upward and backward to be distributed to the viscera, emerges from the most dorsal portion of the abdominal ganglion on the right side of the body (Plate VIII. Fig. 104, Plate IX. Fig. 117). The histological condition of the abdominal ganglion is similar to that of the previously described ganglia of this stage. The fibrous portion, as well as the enlarged cells and nuclei, are especially prominent in the portion of the ganglion which lies to the right of the median plane of the body (Plate IX. Fig 117).

The buccal ganglia (Plate VII. Fig. 95, Plate VIII. Figs. 102, 106, Plate IX. Fig. 120, Plate X. Fig. 121) have become larger, and with their commissure (Plate VIII. Fig. 101, Plate IX. Fig. 120) stretch across the dorsal wall of the neck of the radula sac, to which they are still closely united. The nuclei immediately surrounding the central fibrous portion of the ganglion are already slightly enlarged, though the cells are not so far advanced in their histological differentiation as are those of the other ganglia. A single pair of connectives passes obliquely forward, downward, and outward, to join the buccal to the cerebral ganglia (Plate X. Fig. 121).

By the *sixteenth* and *seventeenth days*, besides a general increase in size of the external organs, the foot gland extends backward much farther than the pedal ganglia (Plate VIII. Fig. 107), and the viscera lie rather more to the left side of the body (Figure G).

The central nervous system (Figure F) now consists of five well developed pairs of ganglia and an azygos ganglion (Figure G). The cerebral ganglia with their commissure form the dorsal portion of three nerve rings, the remainder of which are completed respectively, (1) by the cerebro-pedal connectives, the pedal ganglia, and their commissures; (2) by the cerebro-pleural connectives, the pleural ganglia, the pleuro-visceral connectives, the visceral ganglia, the viscero-abdominal connectives, and the abdominal ganglion; (3) by the cerebro-buccal connectives, the buccal ganglia, and their commissure. The first and second rings are further joined to each other by means of the pleuro-pedal connectives. Each of these three rings encircles the œsophagus. The posterior end of the radula sac in the earlier stages, up to the present one, is usually found to occupy a position *above* the pedal ganglia and their

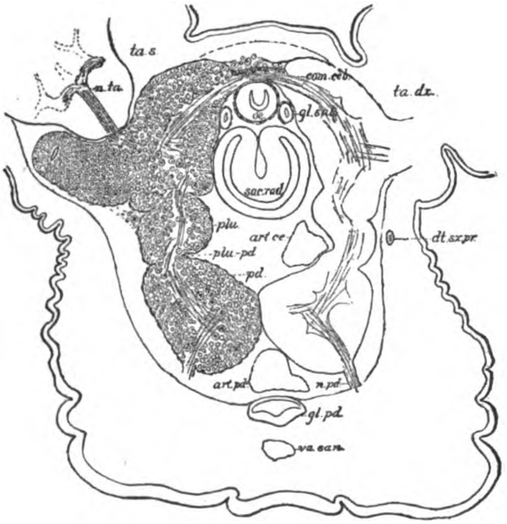

FIGURE F. — Posterior face of a transverse section from an embryo of the *sixteenth day*. × 70.

art. ce.	Cephalic artery.	*œ.*	Œsophagus.
art. pd.	Pedal artery.	*plu.*	Pleural ganglion.
com. ceb.	Cerebral commissure.	*plu.-pd.*	Pleuro-pedal connective.
dt. sx. pr.	Primary sexual duct.	*pd*	Pedal ganglion.
gl. sal.	Salivary gland.	*sac. rad.*	Radula sac.
gl. pd.	Pedal gland.	*ta. dx.*	Right ocular tentacle.
n. pd.	Pedal nerve.	*ta. s.*	Left ocular tentacle.
n. ta.	Tentacular nerve.		

commissures; but with a greater concentration of the nervous ganglia toward one another, the sac is forced to occupy a position *below* the pedal ganglia and their commissures. The relations of the different ganglia to each other is even more definite than before, and can be more readily understood from transverse sections than from sagittal ones. The peripheral nerves from the cerebral, pedal, visceral, and abdominal ganglia are well developed; the principal changes from this time until hatching are histological.

The cerebral invaginations have become narrow and shorter, but are still open to the exterior (Plate X. Fig. 124, *iv.*). The deeper portion of the invagination, that in contact with the proliferated portion of the cerebral ganglion, has become a solid and rounded mass (Plate X. Fig. 122, *lob. lat.*), which is intimately connected with the ganglion by means of fibrous outgrowths from its ganglionic cells. It is composed of small deeply stained cells, which have undergone no such histological change as those which compose the proliferated portion of the brain. It forms a lobe on the antero-lateral face of each cerebral ganglion (Plate X. Figs. 122, 124, 127). From this time forward the principal change in the cerebral sacs consists in the gradual obliteration of the lumen of the invagination. This is usually completed somewhat later in the embryonic life; but, as previously stated, the sacs have in one instance at least been found open several days after hatching. Besides this, there is no other connection now remaining between the ectoderm and any of the ganglia, except such as is effected by means of the peripheral nerves.

The median proliferated portions of the cerebral ganglia now extend dorsally farther than in the last stage, and their commissure is much shorter (Plate VIII. Fig. 105, and Fig. F).

The pedal ganglia (Plate VIII. Figs. 103^a, 109–113) have moved forward, and are broadly in contact with the pleural ganglia. They have become more compact, and rather more triangular in shape, than before. From the ventral portion of each ganglion emerge four or five large nerves, which terminate in the ventral wall of the foot; from the dorso-lateral region two nerves are given off to the lateral walls, and the antero-ventral part of each ganglion tapers off into a stout nerve running forward to the anterior wall. The connectives with the cerebral ganglia are well developed (Plate VIII. Figs. 103, 107).

The pleural ganglia (Plate VIII. Figs. 103^a, 111–113) are nearer to the median plane than previously. The ventral posterior face of each is closely joined to the corresponding pedal ganglion (Figs. 103^a, 112), the dorsal median face to the visceral ganglion (Figs. 103^a, 112, 113), and the anterior face to the cerebral ganglia (Fig. 107). No nerves arise from the pleural ganglia.

The visceral ganglia (Plate VIII. Figs. 103^a, 110–113) have also moved nearer to the median plane. The left ganglion is directly below the œsophagus (Fig. 111 and Figure G), since the latter occupies a position more to the left side of the body than before. The right visceral ganglion still remains larger, and extends farther dorsally than the left (Figs. 103^a, 111, 112). It is nearer the median plane than in the

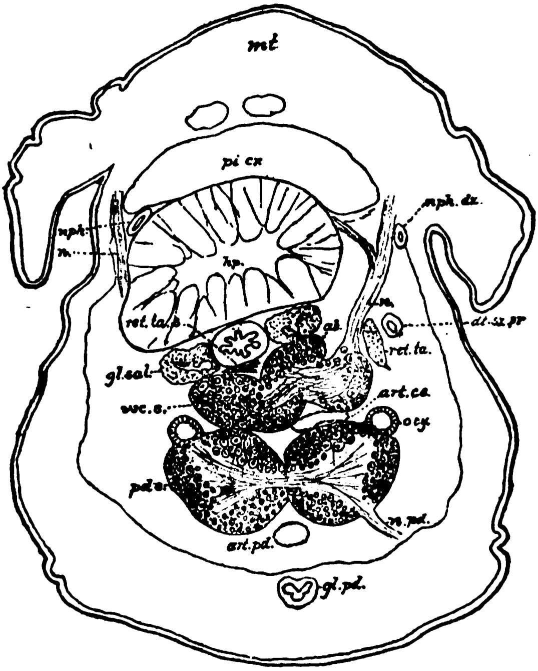

FIGURE G. — Posterior face of a transverse section from an embryo of the *seventeenth day*. × 60.

ab.	Abdominal ganglion.	*n. pd.*	Pedal nerve.
art. ce.	Cephalic artery.	*nph.*	Nephridial organ.
art. pd.	Pedal artery.	*nph. dx*	Right nephridial organ.
dt. sx. pr.	Primary sexual duct.	*o cy.*	Otocyst.
gl. sal.	Salivary gland.	*pd. s.*	Left pedal ganglion.
gl pd.	Pedal gland.	*pi. cr.*	Pericardium.
hp.	Liver.	*ret. ta.*	Retractor muscle of right ocular tentacle.
mt.	Mantle.	*ret. ta. s.*	Retractor muscle of left ocular tentacle.
n.	Nerve.	*vsc. s.*	Left visceral ganglion.

stage last described (Figure D., page 190); it lies in front and only a little to the right of the abdominal ganglion (Fig. 111).

The abdominal ganglion (Plate VIII. Figs. 109–111) is less elongated than in the last stage (Fig. 104). It is wedge-shaped, and appears as though crowded in between the two visceral ganglia from behind and above. It is so intimately connected with these ganglia that it almost appears to form a part of them (Fig. 111). But the presence, between the ganglionic masses, of connective-tissue cells, which reach nearly to the connectives, enables one to make out with some certainty the extent of each of the three ganglia. Since the planes which separate them are oblique to the transverse planes of the body, these boundaries are not always readily seen in cross sections. The right and left visceral ganglia have no *direct* commissural nerve fibres uniting them; they are joined only by such fibres as pass through the abdominal ganglion.

The buccal ganglia (Plate VIII. Fig. 108, Plate X. Fig. 124) are now entirely separated from the dorsal wall of the radula sac, from which they arose, and are surrounded by a layer of connective-tissue cells. The differentiation of their ganglionic cells is well advanced.

Summary.

1. In Limax maximus the whole of the central nervous system arises directly from the ectoderm.

2. The cerebral ganglia originate in part as a pair of true invaginations, one on each side of the body in front of the pleural groove and behind and below the bases of the ocular tentacles. In the course of their development, the neck of each invagination becomes a long, narrow tube-like structure, which remains open throughout the period of embryonic life. The main part of the cerebral ganglia is formed from cells which are detached at an early period from the deep ends of these cerebral invaginations, or from neighboring ectoderm; the portions which persist as the walls of the infoldings finally form distinct lateral lobes of the brain.

3. All the other ganglia originate by cell proliferation from the ectoderm without invagination.

4. The ganglia arise separately, and, with the exception of the abdominal and mantle ganglia, in pairs, one on each side of the body. Their connection with each other is the result of a secondary process in the development, — the outgrowth of nerve fibres.

In advanced stages, the central nervous system consists of five pairs of ganglia and an azygos ganglion. Together these form three complete rings surrounding the œsophagus.

The relative positions of the ganglia are best appreciated from cross sections. In passing from behind forward, they are encountered in the following order: (1) the pair of pedal ganglia, which lie under the radula sac, and are joined to each other by an anterior and a posterior commissure; (2) one abdominal ganglion a little to the right of the median plane; (3) a pair of visceral ganglia occupying the posterior angle formed by the outgrowth of the radula sac from the œsophagus. They are separated by the abdominal ganglion, from which connectives pass to them; (4) a pair of pleural ganglia, not joined by a commissure, and not giving off nerves. They are united by means of connectives to the pedal, visceral, and cerebral ganglia of the same side; (5) a pair of cerebral ganglia, with their supra-œsophageal commissure and connectives to the pleural, pedal, and buccal ganglia; (6) a pair of buccal ganglia, with a commissure under the œsophagus posterior to its connection with the sac of the radula.

The mantle ganglion lies far back, and is joined to the abdominal ganglion by a large nerve.

It seems as if there could be no doubt that the infolding of the ectoderm of the anterior wall of the respiratory cavity on the right side of the body gives rise to the special-sense organ discovered by Lacaze-Duthiers ('72, pp. 483–494). It corresponds in its position and its connection with the right visceral ganglion to his description of the adult, and also to Fol's description ('80, pp. 166–168) of the origin and position of that organ in the aquatic pulmonates.

As is well known, Limax belongs to that group of Gastropods in which all the nerve centres, except the cerebral and buccal, lie on the ventral side of the intestinal tube; not to the group in which the connection between the right pleural and right visceral ganglia passes above the œsophagus, and in which that of the left lies below it. Limax, therefore, is not directly referable to Von Jhering's group of Chiastoneura, although the want of symmetry in the position of its ganglia does not allow one to say that it is orthoneuric.

The Gastropod in which the details of the origin and fate of the nervous centres have been most carefully studied is Bithynia, a chiastoneuric form, in which Sarasin has found that the abdominal ganglion is joined to the right visceral ganglion *only*, and is located at the fundus of the gill cavity. The relation is different from that found in Limax maximus, where the abdominal ganglion is intimately fused with the right visceral, and is *also* in close connection with the left visceral ganglion.

As was to have been anticipated, the abdominal ganglion of Limax corresponds more nearly in position to that in Lymneus and other fresh-water pulmonates, as described for the adult by Lacaze-Duthiers ('72, pp. 437–500).

Of the authors who have studied the origin and development of the *cerebral ganglia* in Mollusks, Fol ('80, pp. 168, 169, 193–195) is the only one who has pursued his investigations on Limax maximus. He says ('80, p. 193): "Vers l'époque de la fermeture de la vésicule oculaire, se montrent deux autres enfoncements de l'ectoderme. L'un des deux, assez vaste et situé à la base du tentacule, à son bord intérieur, est l'origine du ganglion cérébroïde; je le décriai plus loin. L'autre enfoncement, plus petit, est situé au-dessous de ce dernier, à la base du pied, et mène à la constitution de la vésicle auditive."

As to the method by which the cerebral ganglia originate, this agrees in part with that which I have found; but as to the time of origin, my investigations lead me to a different conclusion. The otocysts are present as small groups of cells (Plate I. Fig. 4), and the cellular elements which go to form the beginning of the pedal ganglia are also being proliferated (Fig. 3), before there is a trace of the invaginations which go to form the cerebral ganglia (Fig. 2).

A little later the otocysts assume the form of closed vesicles, unconnected with the ectoderm (Plate I. Fig. 9), while the cerebral invaginations are now seen as shallow pits (Fig. 6). Therefore, in Limax maximus the formation of both pedal ganglia and otocysts precedes that of the cerebral invaginations.

Sarasin ('82, pp. 1–68) maintains that in Bythinia tentaculata there are no invaginations to form the cerebral ganglia. They arise as thickenings of the ectoderm, one on each side of the body, which he calls *die Sinnesplatte.*

In the recent researches of the Sarasin brothers ('87, pp. 600–602, '88, pp. 59–69) on Helix Waltoni, of Ceylon, it is asserted that each of the cerebral ganglia is at first represented by a group of cells derived from the part of the ectoderm called "Sinnesplatte" before there is any invagination. There are two groups of these cells, one on each side of the body. Somewhat later two infoldings arise from each Sinnesplatte, one above the other. These infoldings become long, narrow "cerebral tubes," the deep ends of which are enlarged ('88, Fig. 24). From their inner ends a rapid cell proliferation takes place, the products of which join the cerebral cells already in position. The invaginated portions later form the "accessory lobes" of the brain. At a late stage only one pair of tubes remains open to the exterior, and the openings to these are closed before the end of embryonic life. The Sarasins ('88, p. 61) do not know the precise time at which they are closed, but are certain that the openings do not persist. They express their belief that the cerebral tubes are homologous with the organs of smell in Annelids, which, according to Kleinenberg's studies on Lopadorhynchus, also originate as invaginations of the Sinnesplatte, and by cell proliferation furnish a part of the material for the brain.

Prior to any knowledge of the investigations on Helix by the Sarasins, I found very similar conditions in Limax maximus. In this case, however, there is but one invagination of the ectoderm on each side of the body. It corresponds in position to those described in Helix, being perhaps the equivalent of the upper or larger invagination in that species.

The invaginations in Limax have the form of shallow pits before any other ganglionic cells are to be seen. The cell proliferation, which results in the production of the main portion of the ganglia, takes place during their ingrowth. Possibly the proliferation from the depression between labial tentacle and upper lip represents what was originally a true invagination, and corresponds to the lower of the two invaginations described by the brothers Sarasin. In Limax maximus the external openings persist until a late stage, and occasionally even after hatching. Here, also, the invaginations form a lobe of the brain, exactly as in the case of Helix (Sarasin, '87, p. 601).

Two well developed "Seitenorgane" were found by the Sarasins ('88, p. 54) in Helix Waltoni, situated near each other in the "sense-plate"; and they think (p. 60) that these may correspond in position to the cerebral tubes of later stages.

The groups of cells embedded in the ectoderm, from which, in my opinion, the greater part of the nervous system in Limax maximus takes its origin, resemble both in the arrangement of the cells and their histological condition the "Seitenorgane" described by the brothers Sarasin ('88, pp. 53–57). But I have never observed bristles, or other terminal structures, projecting toward the outer world. Moreover, in Limax unmodified ectodermic cells usually lie between these groups of large cells and the outer surface of the body.

The Sarasins ('88, p. 57) consider these clusters of cells homologous with the "taste-buds" and "lateral organs" of vertebrates, and say that they are to be found in and at the margin of the Sinnesplatten, and along the sole of the foot, — more rarely on the sides of the foot. I think these organs are probably the same as those which I have seen in Limax, and to which I attribute simply the function of contributing to the formation of the ganglia.

Salensky ('86, pp. 685–690) describes the cerebral ganglia of Vermetus as arising from a pair of ectodermic thickenings, which early show pocket-like invaginations, and become deeper and narrower. From the inner ends of these invaginations are formed the main portion of the ganglia. The latter are united to each other by a very small commissure, composed of fibrous prolongations of the ganglionic cells surrounded by other nerve cells.

The principal difference between the method of development in Vermetus and that in Limax maximus consists in the fact that the detachment of the deep portion of the invaginations to form the ganglia in Vermetus is not effected until the invaginations have reached their ultimate size, whereas in Limax the detachment of cells from the invaginated area begins as early as does the invagination, and accompanies it during the whole of its formation.

Kowalesky ('83^a, pp. 1–54) found in Dentalium two deep invaginations, which he calls the "sincipital tubes," one on each side of the head region, a little ventral to the middle of the velar area. From the posterior deep ends of these sacs the cerebral ganglia are subsequently formed; but he is uncertain whether all the cells concerned in the involution share in the formation of the ganglia. If his Figure 65 is compared with Figures 27 and 33 A in Salensky's paper, the close resemblance in the method of origin of the cerebral ganglia in the two types becomes apparent.

Fol ('80, pp. 169, 170) asserts that the *pedal ganglia* of the aquatic pulmonates appear as condensations in an already formed mesoderm, and that they are nearer the pharynx than the ectoderm when they begin to be discernible. "One may therefore say," he adds, "that these ganglia arise from the mesoderm without prejudging the unsettled question, viz. from which of the primordial layers arises the mesoderm which forms them." Of the pedal ganglia of the terrestrial pulmonates, he says that they are diffentiated *en lieu et place* in the midst of the mesodermic tissues of the foot.

With this I cannot agree, although I admit that at the time when the groups of cells which form the ganglia begin to be proliferated from the ectoderm, it is extremely difficult to distinguish them from the mesodermic elements (Plate I. Fig. 5). It is to be observed, however, that Fol considers it an unimportant distinction, whether the ganglia are formed from groups of mesodermic cells which have themselves recently originated from the ectoderm, or by a proliferation of cells directly from the ectoderm.

I am unable to reconcile the account of the development of the pedal ganglia in Bithynia given by P. Sarasin ('82, pp. 47–49), with the conditions seen in Limax; nor can I think it probable that any considerable difference exists between nearly related mollusks in regard to the *place* whence the ganglionic cells arise. Sarasin maintains that in Bithynia the pedal ganglia arise from a *single median thickening of the ectoderm of the dorsal wall of the foot,* in the region where that wall bends over to become continuous with the posterior wall of the visceral sac. Anteriorly, in the region of the oral invagination, this median band of cells forks, and each branch becomes joined to the corresponding cerebro-pleural cell mass by a slender cord of cells. Subsequently, the posterior unique portion of the proliferated cell mass is completely divided into lateral branches by a separation which progresses from in front backward. It seems to me that, according to this account, both the pedal ganglia must be regarded as arising from a common mass of cells, and that they are not from the beginning wholly separate, as I maintain for Limax.

The relative positions of pedal ganglia and otocysts present, to my mind, a serious objection to Sarasin's view, which may not have seemed so important to him on account of his uncertainty about the origin of the otocysts. I believe it is sufficiently evident that the otocysts do not arise, as Sarasin thinks probable, from the cerebro-pleural proliferations, but independently, and from the dorso-lateral wall of the foot in the region of the "pleural groove." They ultimately lie immediately dorsal to the corresponding pedal ganglia. If Sarasin's view as to the origin of the pedal ganglia as a *median* dorsal proliferation were correct, the ganglia would have to migrate to a lower plane than that occupied by the otocysts. But there is no evidence either in Limax or the figures given of Bithynia which would confirm such a supposition. As further corroboration of my opinion that the pedal ganglia arise from the *ventral* and lateral walls of the foot, I would cite the conclusion reached by Salensky ('86, pp. 691, 692) for Vermetus. He has shown that the pedal ganglia originate from the ventral wall of the foot, in a region and by a method corresponding to that seen in Limax maximus, as will be seen by comparing his Figures 21 C to 23 with my Plate I. Figs. 5 and 7, and Plate IV. Fig. 57. The only important difference between Vermetus and Limax lies in the fact that, in the case of the former, the cells forming the ganglion remain from the beginning a more compact mass than they do in the latter.

No one except Lacaze-Duthiers ('72, pp. 456, 457) has mentioned the existence of more than a single pedal commissure. He maintains that there are in Lymnæus as many as *three*. After speaking of the cerebral ganglia as being connected by one commissure, he goes on to say (p. 456), "Au contraire les ganglions pédieux ont trois commissures réelles." He seems, however, uncertain as to whether the most *posterior* ought to be considered a true commissure: "La troisième commissure mérite-t-elle bien ce nom? elle est constante dans les Pulmonés et se présente sous la forme d'un petit nerf grêle transversal naissant à peu près à la hauteur du troisième nerf pédieux inférieur; elle donne vers son milieu naissance à un filet nerveux trés-délié, impair médian que l'on suit dans les tissus de la fosse pédieuse sans trop pouvoir définir et limiter exactment son rôle." (p. 457.) His investigations were made exclusively upon the adult.

In Limax maximus two commissures are certainly distinguishable during a greater part of the embryonic life; no trace of a third has been seen. The adult has not been studied.

None of these authors, with the exception of Sarasin, say anything conclusive concerning the origin of the *remaining ganglia*, although Salensky (86, p. 697) speaks as if the pleural ganglia of Vermetus originated in the cerebro-visceral connectives, which are shown in his Figures 31 B to 31 F.

Sarasin asserts ('82, pp. 46, 47) that in Bithynia the pleural ganglia originate as part of the "Sinnesplatte," from which the cerebral ganglia arise, and that these ganglia, cerebral and pleural, are so closely fused with each other in the later stages of development as to form on either side of the body a single mass.

I believe that they arise in Limax maximus by cell proliferations from the lateral walls of the body, behind the cerebral ganglia, and just above the pleural groove; they are closely connected (not fused) with the cerebral ganglia only in late stages.

Sarasin ('82, pp. 50–52) says that the visceral ganglia in Bithynia arise by cell proliferation from the dorsal margin of the ventral wall of the head or trunk region, above that which I have called the pleural groove. Further, that the right visceral (or supra-intestinal) ganglion is connected by a nerve fibre to the olfactory ganglion under the gill cavity. Farther back than the visceral ganglia he finds a median proliferation of cells lying at the ventral margin of the gill cavity, from which the abdominal ganglia arise. He asserts that there are two abdominal ganglia, — one connected with the supra-intestinal ganglion, the other with the sub-intestinal ganglion.

In Limax maximus the visceral ganglia and the abdominal ganglion arise by the same method as that described by Sarasin; but the former are produced from the lateral walls of the head region, above the pleural groove, one on each side of the body. The right ganglion in later stages is more dorsal than the left. It appears to be formed in part from the inner wall of the respiratory cavity, to which it remains connected by a nerve. It is in this region that is developed an organ which I believe to be the olfactory organ of Lacaze-Duthiers.

There is only one abdominal ganglion; this takes its origin a little to the left of the median line of the body, from the anterior margin of the body wall immediately above the pleural groove.

Sarasin ('82) is the only author who gives attention to the origin of the buccal ganglia. He describes them as arising in exactly the same manner, and in the same situation in relation to the walls of the radula sac and the œsophagus, that they do in the case of Limax maximus.

CAMBRIDGE, November, 1889.

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EXPLANATION OF FIGURES.

All the figures were drawn with the aid of the camera lucida, and were made from preparations of Limax maximus.

INDEX TO STAGES.

The Roman numerals indicate Plates. The Arabic numerals, Figures; those which are enclosed in a parenthesis belong to the same specimen. Skeleton numbers on the plates refer to the number of the section in its series.

6th day. $\left(\frac{\text{I.}}{\text{1, 5}}\right), \left(\frac{\text{I.}}{\text{2–4}}\right).$

7th " $\left(\frac{\text{I.}}{\text{6–9}}\right), \left(\frac{\text{I.}}{\text{10–13}}\right), \left(\frac{\text{II.}}{\text{15, 17, 18}}\right), \left(\frac{\text{IV.}}{\text{53, 55–57}}\right), \left(\frac{\text{IV.}}{\text{54}}\right).$

8th " $\left(\frac{\text{II.}}{\text{14, 16, 19}}\right).$

9th " $\left(\frac{\text{II.}}{\text{20–24}}, \frac{\text{III.}}{\text{25–27}}\right), \left(\frac{\text{V.}}{\text{60}}\right).$

10th " $\left(\frac{\text{III.}}{\text{28–31}}, \frac{\text{IV.}}{\text{58, 59}}, \frac{\text{V.}}{\text{61, 63}}\right).$

11th " $\left(\frac{\text{III.}}{\text{32–47, 51}}, \frac{\text{V.}}{\text{62, 64, 67}}, \frac{\text{VI.}}{\text{70–73}}\right), \left(\frac{\text{V.}}{\text{68, 69}}, \frac{\text{VI.}}{\text{77–80}}\right).$

12th " $\left(\frac{\text{III.}}{\text{48, 49}}, \frac{\text{V.}}{\text{65, 66}}, \frac{\text{VII.}}{\text{81, 82}}\right), \left(\frac{\text{III.}}{\text{50, 52}}, \frac{\text{VII.}}{\text{85–94}}\right), \left(\frac{\text{VI.}}{\text{74–76, }80^{a}}\right), \left(\frac{\text{VII.}}{\text{83–84}}\right).$

14th " $\left(\frac{\text{VII.}}{\text{95}}, \frac{\text{VIII.}}{\text{96, 101, 102}}, \frac{\text{IX.}}{\text{114}}\right), \left(\frac{\text{VIII.}}{\text{97–100, 104, 106}}, \frac{\text{IX.}}{\text{115–120}}, \frac{\text{X.}}{\text{121, 123, 125, 126}}\right).$

16th " $\left(\frac{\text{VIII.}}{\text{107.}}\right), \left(\frac{\text{X.}}{\text{124}}\right).$

17th " $\left(\frac{\text{VIII.}}{\text{103, }103^{a}\text{, 105, 108–113}}, \frac{\text{X.}}{\text{122, 127}}\right).$

ABBREVIATIONS.

The right side of the animal is indicated by the letters dx., the left side by s. These letters are usually affixed to one or more of the abbreviations used to designate organs. The skeleton figures immediately under the number of a figure on the plate indicate the number of the section in the series to which the figure belongs. Consult also "Index to Stages" (p. 207).

ab.	**Abdominal ganglion.**	*lab.*	**Upper lip.**
ab.-vsc.	**Abdomino-visceral connective.**	*lns.*	**Lens.**
an.	**Anus.**	*lob. lat.*	**Lateral lobe of brain.**
buc.	**Buccal ganglion.**	*loph. cil.*	**Ciliated ridge.**
cav. mt.	**Mantle cavity.**	*mt.*	**Mantle.**
ceb.-buc.	**Cerebro-buccal connective.**	*n.*	**Nerve.**
ceb. dx.	**Right cerebral ganglion.**	*nph-*	**Nephridial organ (primitive kidney.)**
ceb. s.	**Left cerebral ganglion.**	*oc.*	**Eye.**
ceb.-pd.	**Cerebro-pedal connective.**	*o cy.*	**Otocyst.**
ceb.-plu.	**Cerebro-pleural connective.**	*œ.*	**Œsophagus.**
cnch.	**Shell gland.**	*pd.*	**Pedal ganglion.**
com. a.	**Anterior pedal commissure.**	*pes.*	**Foot.**
com. buc.	**Buccal commissure.**	*plu.*	**Pleural ganglion.**
com. ceb.	**Cerebral commissure.**	*plu.-pd.*	**Pleuro-pedal connective.**
com. pd.	**Pedal commissure.**	*plu.-vsc.*	**Pleuro-visceral connective.**
com. pd. a.	**Anterior pedal commissure.**	*pr f.*	**Cell proliferation.**
com. pd. p.	**Posterior pedal commissure.**	*rad.*	**Radula sac.**
dt. sx. pr.	**Primary sexual duct.**	*ret. ta.*	**Retractor muscle of tentacle.**
dx.	**Right.**	*s.*	**Left.**
en.	**Entoderm.**	*sul. plu.*	**Pleural groove.**
gl. pd.	**Pedal gland.**	*ta.*	**Ocular tentacle.**
gl. sal.	**Salivary gland.**	*ta.'*	**Labial tentacle.**
gn.	**Ganglion.**	*vsc.*	**Visceral ganglion.**
iv. ceb.	**Cerebral invagination.**	*vsc.-plu.*	**Viscero-pleural connective.**

PLATE I.

All the figures of this plate were made from material killed in Perenyi's fluid, and all except Fig. 1 are magnified 250 diameters.

Fig. 1. A small portion of Fig. 5 more highly magnified to show the cell proliferation for the right pedal ganglion.

" 2. Posterior face of a transverse section from an individual about *six days* old. The section passes anterior to the "pleural groove," and through the region where the cerebral invaginations subsequently arise; the left side is cut a little anterior to the right. Stained in alcoholic borax-carmine.

" 3. A section from the same individual posterior to the pleural groove in the region of the cell proliferation for the pedal ganglia.

" 4. A section from the same, still farther back.

" 5. Transverse section from an embryo a few hours older than the preceding, in the region of the proliferation to form the pedal ganglion. Stained in alcoholic borax-carmine.

" 6–9. The left surface of sections parallel to the sagittal plane from an embryo of the *seventh day*. Figs. 6, 8, and 9 represent respectively the 11th, 16th, and 18th sections of the series, and are from the left half of the embryo. Fig. 7 is from the right half, and passes through the right otocyst. Stained in Czoker's cochineal.

" 10–13 exhibit the right surface of sections from another individual (between the *seventh and eighth days*) cut parallel to the sagittal plane, the anterior portion a little in advance of the posterior. Fig. 10 is a section passing through the proliferation forming the right visceral ganglion. Figs 11 and 12 are two successive sections passing through the left visceral ganglion; the latter also passes through the left otocyst. Fig. 13 shows the region of the forming abdominal ganglion. Stained in picrocarminate of lithium. In both these individuals the left ganglia and otocysts are more developed than the right.

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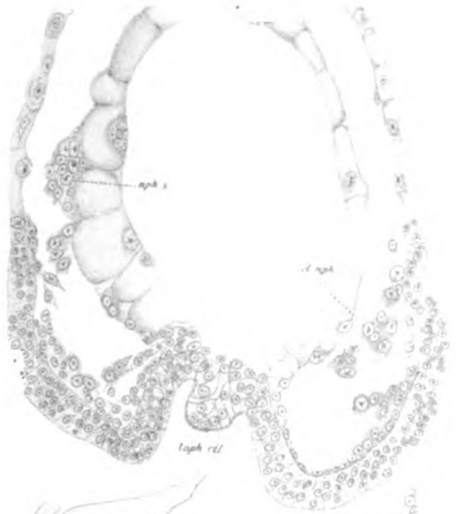

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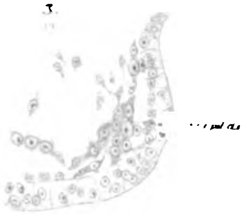

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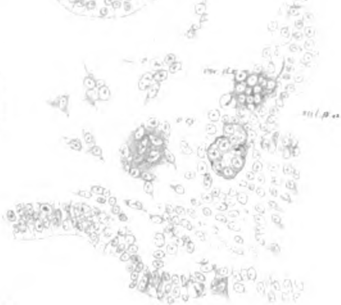

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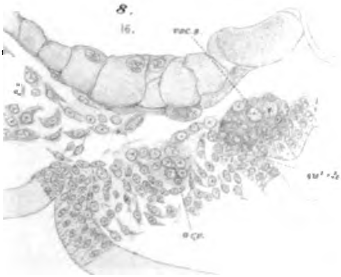

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PLATE II.

All the figures of this plate are magnified 250 diameters.

Fig. 14. **A section parallel to the sagittal plane from an individual of the *eighth day*. It passes through the cerebral and pleural ganglia of the left side of the body, and also shows four cells of the left otocyst posterior to the pleural groove. The material was killed in 0.33% chromic acid, and stained in alcoholic borax-carmine.**

" 15. **The left surface of a section cut parallel to the sagittal plane from an embryo of the *seventh day* (but more advanced than in Figs. 6–9), passing through the cerebral invagination and a group of cells belonging to the proliferated portion of the cerebral ganglion of the right side. The material was treated as in that of Fig. 14.**

" 16. **A section from the same individual as Fig. 14, passing through the cell proliferation to form the visceral ganglion of the right side.**

" 17 and 18 are from the same individual as Fig. 15.

" 17. **A section passing through the visceral ganglion and the external opening of the nephridial organ of the right side.**

" 18. **The second section nearer the median plane than Fig. 17, showing the cell proliferation to form the right visceral ganglion.**

" 19. **From the same individual as Fig. 14, showing the cerebral invagination and proliferation of the right side, and also a cross section of the primitive kidney.**

" 20–24. **The anterior surfaces of transverse sections from an embryo of the *ninth day*. Material killed in Perenyi's fluid, and stained in alcoholic borax-carmine.**

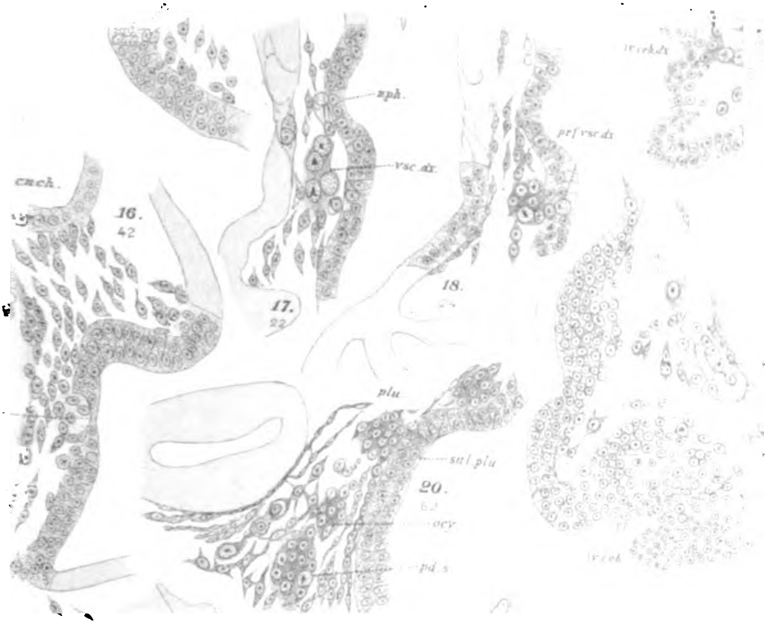
" 20. **Portion of a section which passes through the proliferation of cells forming the pleural ganglion (dorsal to the pleural groove), and through the pedal ganglion and the otocyst of the left side.**

" 21. **The 37th section, which passes through the cerebral commissure and shows the proliferation of cerebral cells on the left side.**

" 22. **The 51st section, which passes through the buccal ganglion of the right side.**

" 23. **The 69th section, showing the unsymmetrical position of the visceral ganglia and a cross section of the right nephridial organ.**

" 24. **The 75th section of the series, passing through the abdominal ganglion and the invagination to form the mantle cavity. It is in the region where the anterior portion of the embryo is bent backward over the foot by the nutritive sac; the foot is not represented in the figure.**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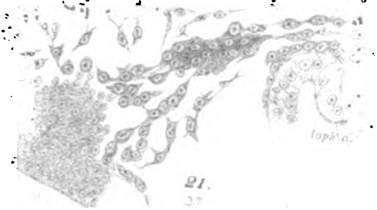
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PLATE III.

Figs. 25–27 are from the same individual (*ninth day*) as Figs. 20–24 on Plate II. They are magnified 83 diameters.

" 25. This section passes through the left cerebral ganglion, and the cerebral invagination of the right side.

" 26 shows, in addition to the cerebral invagination, that of the right eye (at the left of the figure).

" 27. Section passing through the pedal ganglia and their anterior commissure. It shows a cross section of the œsophagus, the radula sac, and the right otocyst.

" 28–31. The left surface of sections parallel to the sagittal plane from an embryo of the *tenth day*. (Figs. 58, 59, Plate IV., and Figs. 61, 63, Plate V., also belong to this series.) This individual was killed in Perenyi's fluid, and stained in picro-carminate of lithium. × 100.

" 28 and 29 are successive sections passing through the invaginations of the cerebral ganglion and the eye of the left side.

" 30 shows a cross section of the cerebral commissure.

" 31. The second section nearer the median plane than Fig. 30, showing the cerebral commissure, the position of the right visceral ganglion, and the anus already open to the exterior.

" 32–47, 51. The left surface of sections cut parallel to the sagittal plane, from an embryo of the *eleventh day*, magnified 100 diameters. Killed in Perenyi's fluid, stained in Czoker's cochineal. (Sections shown in Plate V. Figs. 62, 64, 67, and Plate VI. Figs. 70–73, also belong to this series.)

" 32–38. Seven successive sections passing through the invagination for the cerebral ganglia of the left side.

" 39. The second section nearer the median plane than Fig. 38, showing the inner sac-like end of the invagination.

" 40. The next section, showing the blind end of the invagination and the proliferated portion of the ganglion.

" 41 and 42. Successive sections (32d and 33d of the series) passing through the left pedal ganglion and the connective between the abdominal and left visceral ganglia.

" 43. Section cutting the abdominal ganglion crosswise.

" 44. The 35th section shows, in addition to the abdominal ganglion, a cross section of the anterior pedal commissure. (The 36th, 37th, 39th, and 40th sections of the series are shown in Figs. 47, 46, 45, and 51, respectively.)

" 45. Section passing through the connective between the abdominal ganglion and the right visceral ganglion.

" 46 shows the abdominal ganglion still connected with the ectoderm.

" 47. The next section to that shown in Fig. 44, passing through the abdominal ganglion.

" 48, 49. The left surface of sections cut parallel to the sagittal plane from an individual of about the *twelfth day*, magnified 100 diameters. Killed in

(See obverse.)

0.33% chromic acid, and stained in alcoholic borax carmine. (Sections shown in Plate V. Figs. 65, 66, and Plate VII. Figs. 81, 82, also belong to this series.)

Fig. 48. A section passing through the cerebral and pleural ganglia of the right side, and also through the abdominal ganglion.

" 49 shows the proliferated portion of the cerebral ganglion and the visceral ganglion of the right side.

" 51. (See explanation of Figs. 32–47.) The section following that shown in Fig. 45. It passes through the connective between the abdominal ganglion and the visceral ganglion of the right side.

" 50, 52. The posterior surface of transverse sections of an embryo at the same stage of development (*twelfth day*) as that represented in Figs. 48 and 49. The ventral portion and the right side cut a little in advance of the dorsal portion and the left side, magnified 100 diameters. Killed in 0.33% chromic acid, stained in alcoholic borax-carmine.

Figs. 85–94, Plate VII., continue this series. The following shows the sequence of the sections: —

Section	77,	101,	103,	109,	110,	112,	113,	117,	125,	126,	128,	146.
Figure	90,	92,	91,	93,	50,	52,	85,	86,	88,	87,	89,	94.

" 50. This section passes through the left pedal ganglion and the abdominal ganglion where the latter is still attached to the ectoderm. The mantle cavity open to the exterior.

" 52. The second section in front of Fig. 50, showing that in this region the abdominal ganglion is free from the ectoderm.

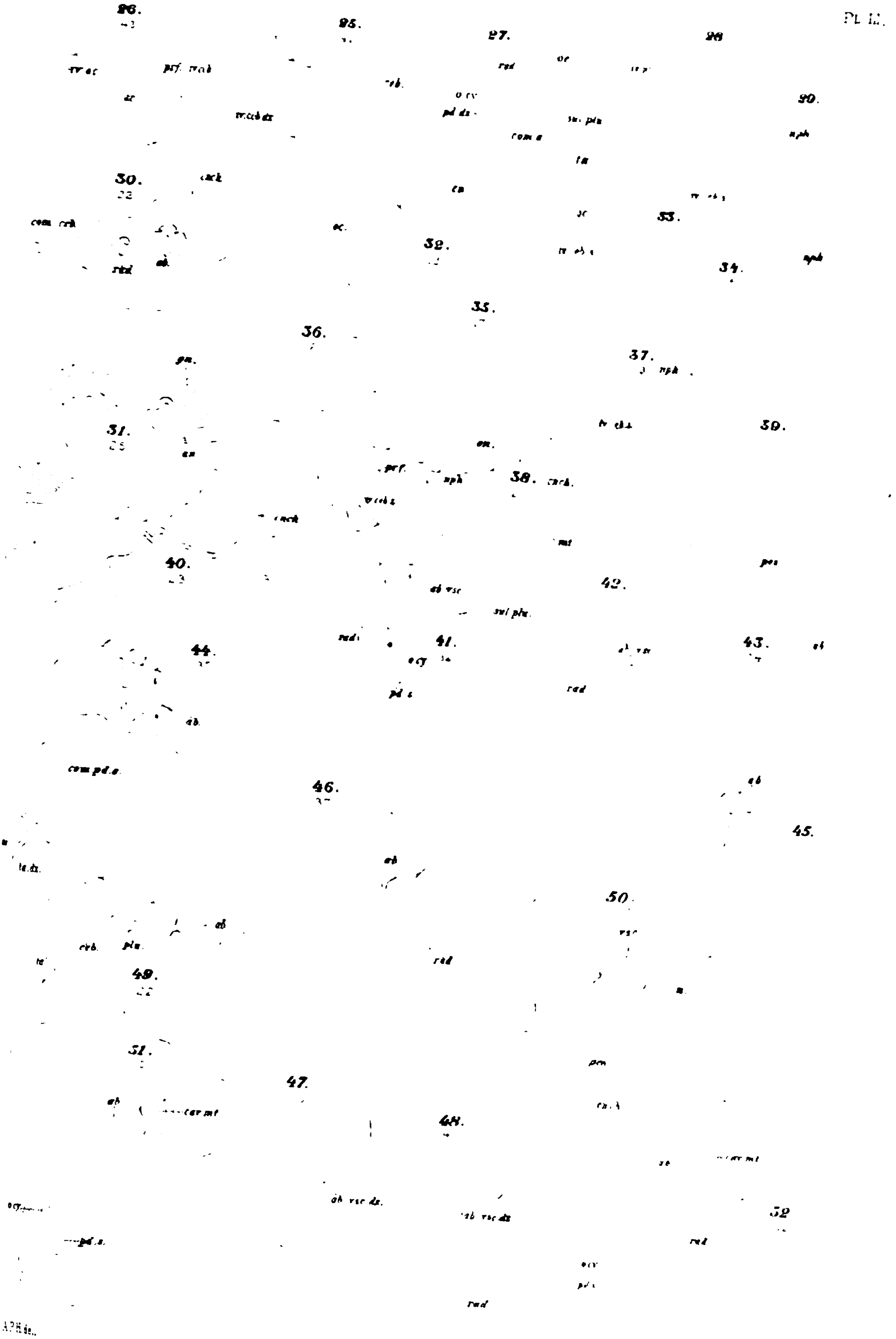

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PLATE IV.

All figures of this plate magnified 250 diameters.

Figs. 53, 56, 57, and 55 are four successive sections from the same embryo. *This was seven days old, but much more advanced than the embryos represented in* Figs. 6–13, 15, 17, and 18. Killed in 0.33% chromic acid, stained in alcoholic borax-carmine.

" 53. Posterior face of a transverse section passing through the visceral ganglia, the external opening of the nephridial organ of the right side, and the opening into the mantle chamber or respiratory cavity. (Compare Figs. 56 and 55.)

" 54. The posterior surface of a transverse section passing through the anterior pedal commissure. Embryo of about the same stage of development as the preceding, and prepared in the same way as that.

" 55. Portion of the third section following that shown in Fig. 53; it passes through the pedal and visceral ganglia of the right side.

" 56 shows both the visceral ganglia.

" 57. Portion of section showing the left pedal ganglion and cell proliferation from the ventral wall of the foot; the visceral ganglion and the external opening of the nephridial organ of the left side are also seen.

" 58, 59. Consult explanation of Figs. 28–31, Plate III.

" 58. Sagittal section passing through the proliferated portion of the right cerebral, pedal, and visceral ganglia and right otocyst. Shows cell proliferation from the ventral wall of the foot, and that the visceral ganglion is attached to the ectoderm at the margin of the mantle cavity.

" 59. A small portion of the section following Fig. 58 to show the right visceral ganglion and its attachment to the ectoderm.

53.

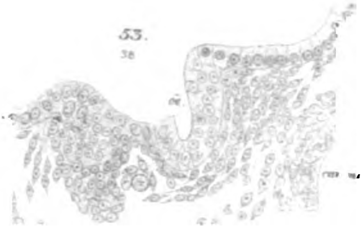

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PLATE V.

All figures magnified 250 diameters.

Fig. 60. The left surface of a section cut parallel to the sagittal plane from an embryo of the *ninth day*. The section passes through a few cells of the cerebral, the pedal, and the visceral ganglia of the right side of the body, and also shows a section of the right otocyst. Killed in Perenyi's fluid, and stained in alcoholic borax-carmine.

" 61. (Consult explanation of Figs. 28–31, Plate III.) Sagittal section (the 22d) to show the abdominal ganglion, which lies embedded in the ectoderm anterior to the pleural groove.

" 62. (Consult explanation of Figs. 32–47, Plate III.) The 32d section of the series, showing a transverse section of the cerebral commissure and a portion of the left buccal ganglion.

" 63. (Consult explanation of Figs. 28–31, Plate III.) The 15th section of the series; it passes through the left cerebral, the pedal, the pleural, and the visceral ganglia, and the wall of the left otocyst.

" 64. (Consult explanation of Fig. 62.) The 24th section; it shows the internal end of the cerebral invagination and the cell proliferation to form the larger part of the brain of the left side.

" 65, 66. Compare explanation of Figs. 48, 49, Plate III.

" 65. The 91st section of the series, showing transverse sections of the buccal commissure and the connective between the abdominal and the left visceral ganglia.

" 66. The 102d section of the series; it passes through the abdominal ganglion.

" 67. (Consult explanation of Fig. 62.) A section through the right visceral ganglion.

" 68. The posterior surface of a transverse section from an embryo of the *eleventh day*. It shows the right visceral and the abdominal ganglia. Killed in Perenyi's fluid, stained in Czoker's cochineal.

" 69. The second section anterior to Fig. 68, passing through the visceral ganglion of the right side.

(Additional sections from this specimen are shown in Figs. 77–80, Plate VI.)

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PLATE VI.

All the figures of this plate were made from material killed in Perenyi's fluid, and all except Figs. 72, 73, and 77 are magnified 250 diameters.

Figs. 70–73. Consult explanation of Figs. 32–47, Plate III.

" 70 shows the left cerebral, pleural, and visceral ganglia in the region of the cerebro-pleural and pleuro-visceral connectives.

" 71. Section passing through the otocyst and the cerebral, pedal, and visceral ganglia of the left side. The visceral ganglion is connected with the ectoderm, and the pleuro-visceral connective is much more elongated than on the *ninth day*.

" 72. A portion of the ventral wall of the foot from the 32d section, to show the cell proliferation for the pedal ganglion. × 665.

" 73. Same as Fig. 72, but from the right side of the body.

" 74–76, 80*. The posterior surface of transverse sections from an individual of the *twelfth day*. The right side cut slightly in advance of the left. Stained in picro-carminate of lithium.

" 74. The 81st section, which passes through the otocysts and both pedal ganglia in the region of their anterior commissure.

" 75 and 76. The 59th and 60th sections of the same series, showing a part of the left side of the embryo in the region of the abdominal ganglion.

" 77–80. (See explanation of Fig. 68, Plate V.) Posterior faces of four successive transverse sections through the mouth of the left salivary duct where it connects with the œsophagus. Fig. 77 shows also the buccal ganglia.

" 80*. (See explanation of Figs. 74–76.) The 107th section of the series. It shows the cerebral commissure, a few cells of the right cerebral ganglion, and the right eye.

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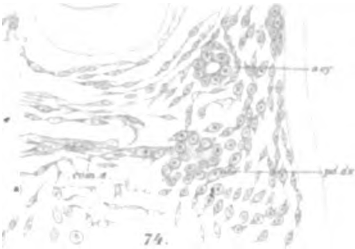

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PLATE VII.

All the figures of this plate, except Fig. 95, were made from material killed in 0.33% chromic acid, and stained in alcoholic borax-carmine. All figures are magnified 250 diameters.

Figs. 81–82. (See explanation of Figs. 48, 49, Plate III.)

" 81. The 114th section of the series; it shows the right cerebral and pedal ganglia, together with the cerebro-pedal connective, the right buccal ganglion, and the abdominal ganglion.

" 82. The 126th section of the series. It passes through a portion of the right cerebral ganglion, the right pleural and the abdominal ganglia, from the last of which a nerve runs dorsalward.

" 83, 84. The left surface of two sections (the 96th and 99th) parallel to the sagittal plane from an embryo of the *twelfth day*.

" 83. The section shows a very small portion of the cerebral ganglion, the pleural and visceral ganglia of the right side in the region of the pleuro-visceral connective, and the abdominal ganglion together with its connective with the right visceral ganglion.

" 84 shows the right visceral and the abdominal ganglia; also, a portion of the connective between the abdominal and the visceral ganglia, and a large nerve extending dorsalward from the latter.

" 85–94. (See explanation of Figs. 50, 52, Plate III.) Transverse sections, *twelfth day*.

" 85. This section (113th) shows a portion of the abdominal ganglion separated from the ectoderm.

" 86 (117th section) shows a small portion of the abdominal ganglion, as well as the pleural and visceral ganglia of the right side, together with their connective.

" 87. (126th section; compare also 125th section, Fig. 88.) A portion of the right visceral ganglion and the large nerve running dorsalward from its left dorsal margin are shown.

" 88 (125th section) shows both visceral ganglia — the left one still connected with the ectoderm — and the left pleural ganglion, together with the pleuro-visceral connective.

" 89. The 128th section, which touches the right visceral ganglion, and a large nerve running dorsalward between mantle cavity and sexual duct from the right dorsal margin of the ganglion.

" 90. The 77th section; it passes through both pedal ganglia and their posterior commissure, which is directly above the blind end of the pedal gland, the tip of which is cut.

" 91. The 103d section, which shows the right pedal ganglion and otocyst.

" 92. The 101st section, which passes through the pedal ganglia and their anterior commissure, above which is the radula sac, and below which a blood-vessel and the pedal gland are to be seen.

(See obverse.)

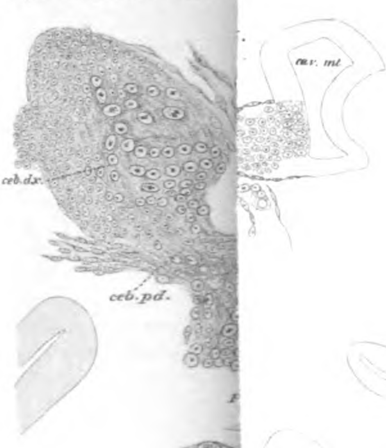
Fig. 93. The 109th section; this passes through the abdominal ganglion at the place of its connection with the ectoderm lining the median wall of the mantle cavity. It also shows a portion of the connective from the abdominal ganglion to the left visceral ganglion.

" 94. The 146th section of the series; it shows a cross section of the neck of the cerebral invagination, and a small portion of the cerebral ganglion of the left side.

" 95. The left surface of the 54th section, from an individual of the *fourteenth day*. The section passes through the right visceral and the abdominal ganglia, showing their close connection with each other at this time, and it also cuts the right buccal ganglion. The material was killed in Perenyi's fluid, and stained in picro-carminate of lithium.

The following figures are drawn from sections of the same series as Fig. 95: Plate VIII. Figs. 96, 101, 102; Plate IX. Fig. 114. The sequence of sections is this: —

Section 52, 54, 56, 66, 82.
Figure 101, 95, 102, 114, 96.



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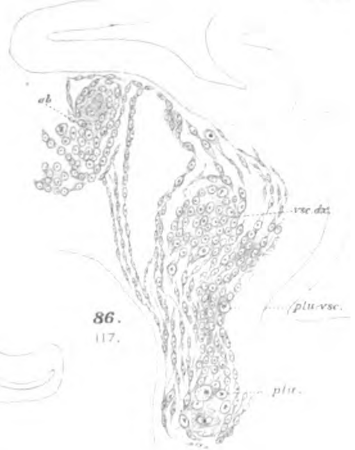

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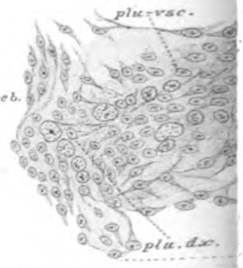

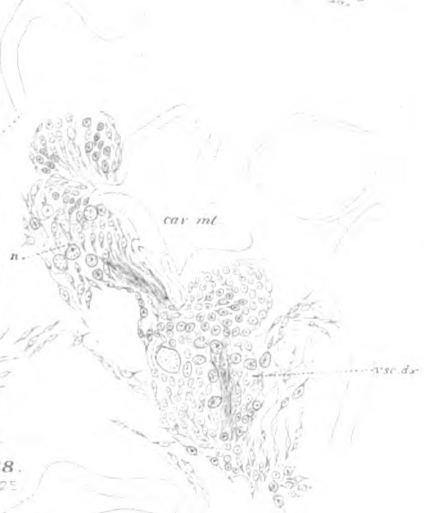

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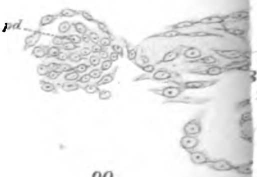

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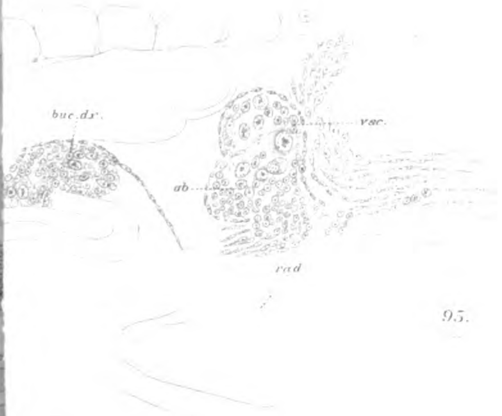

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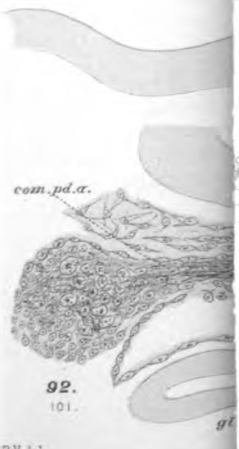

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PLATE VIII.

Fig. 96. (See explanation of Fig. 95, Plate VII.) The 82d section; it passes through the ocular tentacle, showing in section the cerebral invagination and ganglion of the right side. × 100.

" 97–100. Posterior faces of transverse sections, the right side a little in advance of the left, from an embryo of the *fourteenth day*. Killed in Perenyi's fluid, stained in picro-carminate of lithium. — Figs. 104, 106; also Plate IX. Figs. 115–120, and Plate X. Figs. 121, 123, 125, 126, belong to the same series as Figs. 97–100. The sequence of sections is: —

Section	81,	87,	92,	98,	102,	104,	109,	111,	113,	113,	115,	121,	122,	122,	127,	139.
Figure	97,	119,	98,	99,	118,	100,	115,	116,	104,	117,	123,	120,	106,	125,	121,	126.

" 97. The 81st section; it passes through the pedal ganglia, a few sections behind the posterior commissure. × 100.

" 98 and 99. The 92d and 98th sections; they pass through the pedal ganglia between the two commissures. × 100.

" 100. The 104th section, two sections in front of the anterior commissure. It shows the right otocyst in addition to the radula sac and pedal gland. × 100.

" 101, 102. (See explanation of Fig. 95, Plate VII.)

" 101. The 52d section of the series, showing the abdominal ganglion, and a cross section of the cerebral, buccal, and both pedal commissures. × 100.

" 102. The 56th section; it passes through the visceral and buccal ganglia of the right side, and a portion of the abdominal ganglion. It shows the cerebral and pedal commissures, as well as a sagittal section of the foot gland. × 100.

" 103, 103^a. The posterior surfaces of transverse sections from an embryo of the *seventeenth day*. 0.33% chromic acid; alcoholic borax-carmine. — Additional sections from this series are shown in Figs. 105, 108–113, and Plate X. Figs. 122, 127. The sequence of sections is indicated by the following: —

Section	111,	176,	180,	186,	187,	194,	211,	212,	217,	225,	225.
Figure	103^a,	109,	110,	111,	112,	113,	103,	105,	122,	108,	127.

" 103. The section passes through the cerebral ganglia in the region of the cerebro-pedal connective. The wall of the body is not represented, but merely the ganglia, together with the œsophagus, the ducts of the salivary glands, the radula sac, and the right ocular tentacle. × 140.

" 103^a. This section (111th) passes through the pedal, pleural, and visceral ganglia in the region of the pleuro-pedal connective. A large nerve passes from the dorsal margin of each pedal ganglion to the lateral wall of the body. × 83.

(See obverse.)

PLATE VIII. (*continued.*)

Fig. 104. (See explanation of Figs. 97–100.) The 118th section; it passes through the pleural ganglia and the abdominal ganglion. A large nerve connects the abdominal ganglion with a pocket-like infolding from the wall of the mantle cavity. × 100. Figure 117 (Plate IX.) shows a portion of this section more highly magnified.

" 105. (See explanation of Figs. 103, 103ª.) The 212th section; it passes through the cerebral commissure. × 100.

" 106. (See explanation of Figs. 97–100.) This section, the 122d, passes through the right cerebral invagination, the right cerebral and buccal ganglia with their connective, and the right visceral ganglion. It also shows the left pleural and visceral ganglia with their connective. × 100.

" 107. Is a combination of two successive sections cut parallel to the sagittal plane from an embryo of the *sixteenth day*. It shows the cerebral, pedal, and pleural ganglia, with their connectives, and the otocyst of the left side. The position of the pedal gland is shown by dotted lines. Perenyi's fluid; picro-carminate of lithium. × 100.

" 108-113. See explanation of Figs. 103, 103ª.

" 108. The 225th section of the series shows the cerebral invaginations. The right one (an enlarged view of which is seen in Fig. 127) is cut lengthwise, it being still open to the exterior; the left one transversely. The cerebral ganglia and their lateral lobes, and the buccal ganglia with their commissure crossing between the radula sac below and the œsophagus above, are also shown. × 83.

" 109. The 176th section, which passes through the pedal ganglia and the abdominal ganglion. × 83.

" 110. The 180th section; it shows, in addition to the organs seen in Fig. 109, a small portion of the left visceral ganglion and the otocysts.

" 111. The 186th section; it passes through the pedal ganglia, a portion of the pleural ganglion of the right side, both visceral ganglia, and the abdominal ganglion. It also shows the connective from the abdominal to the right visceral ganglion, and a stout nerve arising from the latter. × 83.

" 112. The 187th section shows the pedal, pleural, and visceral ganglia. × 83.

" 113. The 194th section. This shows, in addition to the ganglia, the nerve which arises from the left visceral ganglion. × 83.

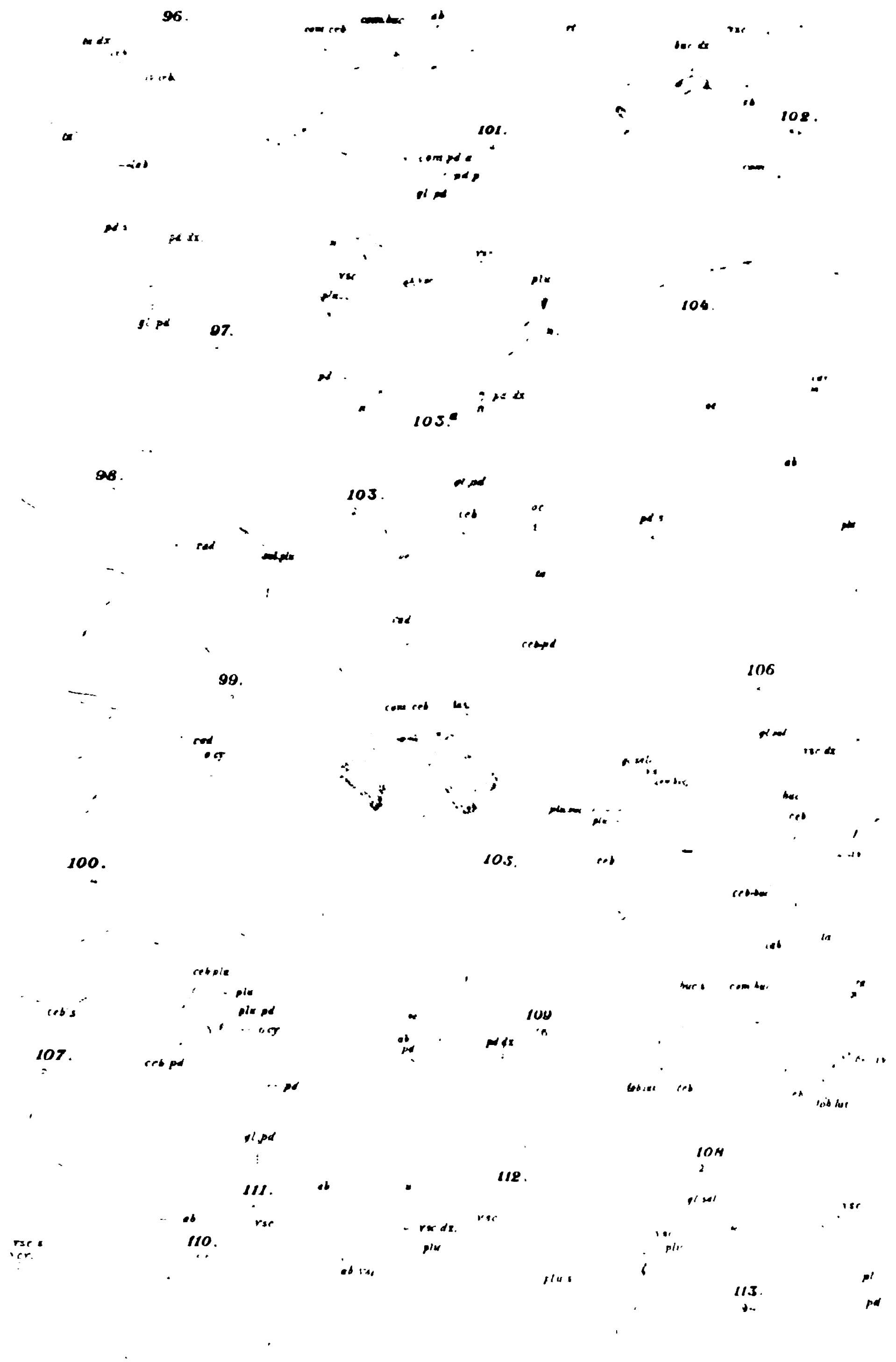
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PLATE IX.

All the figures of this plate are magnified 250 diameters, and were made from material killed in Perenyi's fluid, and stained in picro-carminate of lithium.

Fig. 114. (See explanation of Fig. 95, Plate VII.) The 66th section; it passes through the cerebral, the pedal, the pleural, and the visceral ganglia of the right side in the plane of the cerebro-pedal and cerebro-pleural connectives. It also shows the right otocyst.

" 115–120. See explanation of Figs. 97–100, Plate VIII.

" 115. The 109th section; it shows a portion of the abdominal ganglion at the right of the radula sac.

" 116. The 111th section; it passes through the abdominal and right pleural ganglia.

" 117. The 113th section; it shows the abdominal ganglion where it passes above the radula sac, and a portion of the right pleural ganglion. (Compare Fig. 104, Plate VIII.)

" 118. The 102d section; it passes through the pedal ganglia in the plane of their anterior commissure. It also shows the right otocyst.

" 119. The 87th section. The pedal ganglia in the plane of their posterior commissure.

" 120. The 121st section, which passes through the visceral and buccal ganglia of the right side, and shows a portion of the buccal commissure.

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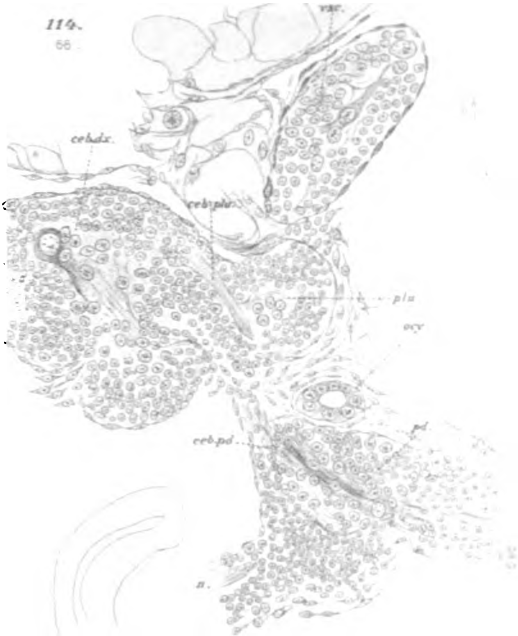

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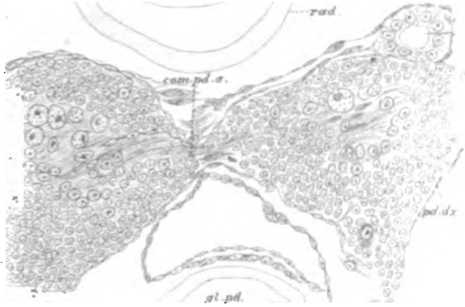

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PLATE X.

Fig. 121. (See explanation of Figs. 97–100, Plate VIII.) The 127th section; it passes through the left cerebral invagination, also through the left cerebral and buccal ganglia, and their connective. × 237.

" 122. (See explanation of Figs. 103, 103^a, Plate VIII.) The 217th section of the series. It passes through the right cerebral ganglion and its lateral lobe; it also shows the ocular tentacle and the wall of the right eye, transverse sections of the œsophagus, salivary glands, radula sac, and primary sexual duct. × 237.

" 123. (See explanation of Figs. 97–109, Plate VIII.) This section passes through the right pleural and visceral ganglia, a small portion of the left pleural and visceral ganglia, and the abdominal ganglion, which lies between the œsophagus and radula sac. × 250.

" 124. The posterior face of a transverse section from an embryo of the *sixteenth day*. The left side is cut a little in advance of the right. The section passes through the cerebral invagination, — still open to the exterior, — the cerebral ganglion of the left side and its lateral lobe, and the left buccal ganglion. It also shows in cross section the duct of the salivary gland, and a small portion of the wall of the radula sac. × 237. Perenyi's fluid; picro-carminate of lithium.

" 125, 126. See explanation of Figs. 97–100, Plate VIII.

" 125. The 122d section; it shows the left pleural and visceral ganglia, with the pleuro-visceral connective, and a small portion of the left cerebral ganglion. × 250.

" 126. The 139th section; it shows in section the left cerebral invagination, the cerebral ganglion, and the cerebral commissure. × 250.

" 127. (See explanation of Figs. 103, 103^a, Plate VIII.) The 225th section; it shows the cerebral invagination, and the right lateral lobe of the brain. (Compare Plate VIII. Fig. 108.) × 237.

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AT HARVARD COLLEGE.
VOL. XX. No. 8.

22

THE PARIETAL EYE IN SOME LIZARDS FROM THE WESTERN UNITED STATES.

BY W. E. RITTER.

WITH FOUR PLATES.

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No. 8. — *The Parietal Eye in some Lizards from the Western United States.* By W. E. Ritter.[1]

With a single though notable exception, the numerous authors who have written on the parietal organ in vertebrates since the papers of de Graaf ('86[a] and '86[b]) and Spencer ('86 and '87) appeared, have agreed that the structure is, or at least was in ancestral vertebrates, an eye. This belief is based entirely on the structure of the organ, no physiological experiments or observations on the habits of the animals possessing it having yet been produced in proof of its function.

Leydig ('89) alone, in a recent preliminary paper on the subject, has denied its optical nature, and has assigned to it an entirely different function; though in a second preliminary, still more recent ('90), he expresses his denial with considerably less confidence. He rejects the eye hypothesis, however, on the same grounds that have led others to adopt it; namely, on the grounds of its structure, and especially of its relation to the brain.

He believes that what is generally held to be an optic nerve is in fact merely a string of connective tissue.

Among those who believe the organ is or has been an eye, there are important differences of opinion as to its present value. By Ahlborn ('84), de Graaf, Spencer, and several other more recent writers, it is believed to be degenerate and entirely functionless in all living vertebrates. Rabl-Rückard ('86) has expressed the opinion that the organ may still be of use in furnishing its possessors with a more delicate means of detecting differences of temperature than exists elsewhere on the body. Béraneck ('87) believes that, while the structure is probably of an optical nature in some vertebrates, it has become so secondarily; that the primitive function of the epiphysis, common to the brains of all vertebrates, was something entirely unknown to us now, though not concerned with vision; but that in the Cyclostomes, the Amphibians, and the Reptiles it has taken on, secondarily, the function and form of an eye.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXII.

But even were it established beyond question that the organ is a degenerate eye, there would still remain several quite distinct and very interesting problems to be solved. The most fundamental of these is probably that of its homology. Much has been written on this question by the various recent authors, but even less unanimity of opinion has been reached here than on the question of its structure and function. The question why the organ has remained so well developed in a few systematically widely separated groups of vertebrates, while in all others the process of degeneration has gone so far as to leave but a mere trace of the proximal portion of the epiphysis, has not been much discussed. It is not my purpose in the present paper to enter upon a discussion of the theoretical questions involved, and they are here adverted to merely to point out the need — as indicated by their importance and the discordance of the opinions now held with regard to them — of a larger body of facts on the subject than we yet possess. For the present, I confine myself to a presentation of the facts observed, and my interpretation of them as bearing upon some of the minor conclusions reached by other writers, hoping to be able to pursue the subject further in the near future, when situated in a region where an abundance and a variety of material, adult and embryonic, can be obtained, and where observations on the habits of the animals can be made.

The present work was undertaken at the suggestion of Prof. E. L. Mark. I wish here to acknowledge my indebtedness to Mr. G. H. Parker, of the Museum of Comparative Zoölogy; to Mr. J. J. Rivers, Curator of the Museum at the University of California; and to Mr. T. C. Palmer, of the United States Department of Agriculture, Washington, for material used; and also to Mr. S. Garman, of this Museum, for assistance in determining the species studied.

A word as to technique. For studying the structure of the retina it is very desirable to remove the great quantity of pigment that invariably obscures the histological elements in this region. Neither nitric nor hydrochloric acid, nor the alkalies, have any visible effect on this pigment, but the desired result was reached by the use of chlorine gas. The mounted, unstained sections were covered by a film of ninety per cent alcohol, and placed in a tight glass chamber, in which was also confined a small vessel containing a mixture of potassium chlorate and hydrochloric acid for generating the gas. By being careful that the slide on which the sections were mounted occupied a perfectly horizontal position, and was so placed that the film of alcohol could not be drawn off by capillary attraction, the film soon became saturated with the gas, and did not need renewing. From forty-five minutes to an hour, depending on the quantity of pigment, was sufficient time in which to accomplish the work. Considerable difficulty was found in removing the chlorine from the sections. As it had thoroughly penetrated the tissue, simple washing, even though prolonged, did not wholly remove it; but by washing carefully, and then leaving the whole slide immersed in ninety per cent alcohol for twelve or fourteen hours, the gas was entirely removed. A good quality of Schällibaum's fixative held the sections perfectly through all this and the subsequent staining.

For decalcifying and hardening the tissues I have found Perenyi's fluid more satisfactory than anything else tried, the two processes being accomplished at the same time by this reagent.

Of the several species of lizards which I have studied I shall describe the structure in only three, namely, Phrynosoma Douglassii, P. coronata, and Uta Stansburiana, these being the only ones that have presented anything new or of special interest.

Phrynosoma Douglassii.

1. *External Appearance.* — Concerning the external appearance of the organ little need be said, since it differs in no essential particular from what has been amply described and illustrated in numerous other lizards. The scale marking the position of the eye is quite conspicuous, especially in very young individuals, where it is of a rather lighter color and larger size, relatively, than in the adult. In old individuals the great development of the surrounding scales and tubercles renders it somewhat less noticeable than it otherwise would be, but it is always readily distinguished, not only by its median position, but also by the absence of pigment and by its translucent appearance.

2. *The Parietal Vesicle.* — Figure 1, drawn from a sagittal section through the dorsal wall of the head, shows the form of the vesicle and its position within the parietal foramen and with reference to the external and internal surfaces of the wall. It lies within the parietal foramen, though extending somewhat above the dorsal surface of the parietal bone, firmly embedded in connective tissue, so that when the wall of the head is separated from the brain the vesicle always goes with the former. The tissues composing the dorsal wall of the head are, excepting the corneous layer of the skin, quite different immediately over the vesicle from those of the surrounding regions. The epidermal layer of the skin

elsewhere sends down irregular cone-shaped masses, which penetrate and become lost in the underlying connective tissue, thus firmly uniting the two layers. Over the vesicle, however, these processes are wholly wanting, the under surface of the epithelial layer being even, and sharply limited from the connective tissue. These processes are especially well developed immediately beyond the margin of the disk of the vesicle, where they carry the cells of the epidermal layer (*e'drm.'*) considerably deeper than their general level. The connective tissue between the vesicle and the epidermal layer is composed of fibres considerably finer and looser than those found in other places, and, furthermore, the fibres are here disposed at various angles to the surface of the skin, whereas elsewhere they are approximately parallel to this surface (*con't. tis.'*). Pigment, which is found in great abundance in the skin in all other regions of the body, is always entirely absent here. It will thus be noticed that each of the tissues over the vesicle is considerably more penetrable to light than are the corresponding ones elsewhere. The connective-tissue fibres immediately around the vesicle are arranged concentrically to its surface, and are, especially in the proximal two-thirds of their extent, considerably finer and closer than elsewhere. A kind of capsule for the vesicle is thus formed, and it is this alone which separates it from the cranial cavity. The fibres of a string of tissue extending from the distal end of the epiphysis can be traced, though with some uncertainty, to this capsule, but I find no indication of their passing through it, or even entering it, though I have given special attention to this point.

The internal surface of the cranial wall in the region of the vesicle presents a depression, which is much less marked, however, than a corresponding one in P. coronata, to be referred to hereafter. Running through the connective tissue at the bottom of this depression, and hence near the deep surface of the vesicle, are found a number of blood-vessels of considerable size and well filled with blood corpuscles (*va. sng.*). The vesicle itself is elliptical in sagittal section, the major axis, 258 μ long in the specimen figured, having the direction of the long axis of the head. In transverse section it is slightly elongated dorso-ventrally, and measures in this axis 171 μ.

The cavity in sagittal section shows a triangular outline, the base of the triangle being on the dorsal or lens side. From this outline in the sagittal section the form gradually changes to that of an ellipse in the last sections on each side that cut the cavity; so that the form of the cavity is approximately that of a broad, flat cone, the base directed outward and the apex inward. The base of the cone is slightly concave, corresponding to the convexity of the inner surface of the lens.

The wall of the vesicle is very distinctly differentiated into lens (*lns.*) and retinal (*rtn.*) portions, the latter forming about two thirds of the whole. The lens is slightly biconvex, the two convexities being very nearly equal. The line of demarcation between the lens and the retina is a sharp one, though the two portions are plainly continuous. The cells composing the lens are large and distinct in outline, each one extending entirely through its thickness (Plate II. Fig. 5, *cl. lns.*). Their nuclei are large, easily stainable, and somewhat granular; they are uniformly situated near the internal ends of the cells. The lens is entirely without pigment.

Figure 5 represents a highly magnified portion of a longitudinal vertical section of the vesicle taken from near the median plane. In the retinal portion six regions or zones may be distinguished. Passing from the external surface toward the cavity, we find (1) a basement membrane (*mb. ba. ex.*). This is very thin, but uniform in thickness, and is of a structureless nature. From many points on this membrane fine processes radiate into the connective tissue enveloping the vesicle (Plate I. Fig. 3, *prc. r.*). These processes do not appear to be of a muscular nature, but rather the same in structure as the basement membrane from which they arise. (2) A zone containing a few scattered nuclei (*nl.'*), and fine-grained sparsely but evenly distributed pigment (*pig.*). No cell boundaries can be made out in this zone. The nuclei, few in number, form a single layer, and are situated near the basement membrane. They are very nearly round, exhibiting no tendency to elongate in the radii of the vesicle. Areas in their centres, which are somewhat more deeply stained than the rest of the nuclei, and which are probably nucleoli, are to be seen. (3) A zone (*z.''*) in which are distinguishable neither cells, nuclei, nor pigment; only a uniform, fine-granular, slightly stainable substance, of much the same nature, apparently, as the cell substance in those regions of the retinal portion in which cell boundaries can be distinguished. Whether or not this zone represents the centrally directed ends of a layer of cells, the nuclei of which are the ones found in zone 2, I am unable to say, but it probably does. (4, 5) The next two zones are distinguished from each other only by the difference in the elements composing them, no distinguishable line of separation existing between the two. The most obvious difference between the constituent elements of these two regions is in the shape of the nuclei, those in zone 4 being approximately spherical (*nl.''*), while those in zone 5 are much elongated in the radii of the vesicle (*nl.'''*). The suggestion at once comes that this difference is due solely to the crowding together of the cells nearest the internal surface of the retina, and hence that the two zones should in reality be regarded as but one. If, however, the difference in shape of the nuclei were the result solely of such crowding, we should find a complete gradation from the spherical to the elongated form in passing from without inward; but such a gradation is not found in fact. Furthermore, on close examination with high powers, it is found that the nuclei differ in structure as well as in form. An irregular stellated area can be detected in the centres of some of the spherical ones which does not exist in the elongated ones; also, the entire substance of the former is slightly more granular than that of the latter. In the fifth zone cell boundaries (though not well shown in the figure) can be quite distinctly traced to the internal basement membrane; but how the cells of the fourth and fifth zones are related I have been unable to determine, since cell boundaries in the fourth zone cannot be traced. (6) The last layer may be designated as an internal basement membrane (*mb. ba. i.*), though it differs somewhat in structure from the external basement membrane, being of a granular nature. It extends over the surface of the lens, as well as over the retina, and is rather more compact in the former than in the latter region. Projecting into the cavity of the vesicle from the retinal portion are found certain structures concerning the nature of which I am not quite sure, but believe them to be secretions from the cells of the fifth zone. They are in general elongated, and pointed at their free ends, though their outlines are ragged and indefinite. They always stain most deeply at their internal free ends. In many cases, as at *, they are seen to be continuous with the cells of the fifth zone through the internal basement membrane. These structures may correspond to what de Graaf has described and figured as existing on the internal surface of the retina of Anguis, and has called "Staafjeslaag," but which Spencer and others believe to be merely a coagulum from the fluid that probably filled the cavity in the recent state. It is, however, scarcely possible to account for the structures here under consideration in this way, as is to be seen from my description and figures of them; furthermore, a coagulum (*cog.*) does exist in addition to these.

Within the substance of the retina (Fig. 5, *va. rtn.*) are found a number of cavities varying in diameter, as measured in the plane of the sections, from 5.5 μ to 22 μ. The sections of these cavities are never quite circular, but are never much elongated. In many, though not in all, an exceedingly thin endothelial lining can be seen, and in a few instances blood corpuscles are found in the cavities (Plate I. Fig. 4, *en'th. va.* and *cp. sng.*). Although none of these cavities were found to extend through more than four or five sections, each 7.5 μ in thickness, and although in no instance was it possible satisfactorily to trace a connection between them and the blood-vessels lying outside the vesicle, it still seems quite certain that they form a network of fine blood-vessels ramifying through the substance of the retina. Owing to the fact that in some instances no lining membrane to these cavities can be found, and that their outlines are not sharply marked, the possibility of their having been artificially produced by the removal of pigment masses suggests itself; but the definiteness of the outline of many others and their endothelial lining membranes, in which much-flattened nuclei are found, strips this conjecture of its plausibility. If these are really blood-vessels, it might appear that some of them would be seen cut longitudinally; and while it is true that in many cases focusing shows the cut walls to be very oblique to the plane of the section, still no sure instance of a vessel cut lengthwise has been seen. When, however, one considers the exceeding delicacy of the endothelial lining, and the fact that no differential staining takes place, it does not seem impossible that such sections may exist, and yet escape detection. These cavities have no regularity of arrangement, but are for the most part confined to zones 2, 3, and 4. In no instance has one been seen confluent with the cavity of the vesicle.

These may possibly correspond to what Owsjannikow mentions as having been seen by him in Chamæleon vulgaris. He says: "Am hintern Rande der Retina findet sich an einigen Schnitten das Lumen eines Rohrs, von dem nicht mit Bestimmtheit gesagt werden kann, ob es einem Blutgefässe oder einem anderen Gewebe angehört." (Owsjannikow, '88, p. 16.)

3. *The Epiphysis.* — Figure 9 (Plate III.) represents a sagittal section of the epiphysis, and so much of the brain as is necessary to show the relation of the former to the latter. The entire structure, or, more properly, the combination of structures that must be considered at this time, presents the form of a curved cylinder, one end of which is produced into a cone, while the other end has a hopper-shaped excavation. In keeping with the usual method of designation, I shall call the whole structure the epiphysis, though, as the sequel will show, it is doubtful if this is justifiable. The excavated end is proximal, the

excavation being the continuation of the cavity of the third ventricle into the epiphysis. The conical end, then, is distal, and rises somewhat above the level of the cerebral hemispheres. The curved axis forms very nearly a segment of the circumference of a circle, and is directed upward and forward from its point of origin from the brain. Continuing anteriorly from the apex of the cone is a string of connective tissue (*con't. tis.*), which passes to the region of the parietal vesicle, and in the distal portion of its course comes close in contact with the dura mater of the brain. The axis of the cylinder, if we consider it as continued to the anterior termination of this connective-tissue string, describes very nearly a semicircumference. The most anterior point in the connection of the epiphysis with the brain is at the junction of the cerebrum with the optic thalamus, somewhat anterior and dorsal to the superior commissure (*com. su.*). For a short distance above its connection with the brain in this anterior part, the epithelial nature of the epiphysial wall is less distinct than at a higher level, where the wall becomes thicker, and is composed of a single layer of more or less cuboid nucleated cells, which stain readily in borax carmine or hæmatoxylin (Plate III. Figs. 8, 9, *e'th.*). Also at this level the wall becomes thrown into a highly complicated system of folds; and it is this folded epithelium, containing within its folds great quantities of blood corpuscles, that forms a large bulk of the whole epiphysis (Figs. 8 and 9, *e'th.* and *cp. sng.*).

In the section represented in Figure 9 no connection exists between the epithelium of the posterior portion of the epiphysis and the brain, and it is doubtful if such connection exists here in any of the sections of this specimen; at any rate, if it does exist, it is exceedingly thin and limited in extent. There is, however, an undoubted connection in this region in P. coronata, which will be described later; but even in this latter species the posterior wall of the epiphysis is much less developed than the anterior wall. The exceedingly thin epithelium that forms the posterior wall in P. Douglassii would, as is evident from its position and from comparison with P. coronata (Plate IV. Figs. 11 and 12), form a connection with the brain roof had not a separation taken place, either artificially or as a result of degeneration. This wall is closely applied to the anterior, concave side of the blood sinus to be presently described, and at a considerable distance above the brain is continuous with the anterior wall of the epiphysis. The space included by these walls is the hopper-shaped excavation in the proximal end of the cylinder already mentioned, — an extension of the cavity of the third ventricle (*vnt.*^{3}) into the epiphysis. Intimately connected with the distal end of the portion of the epiphysis thus far described is found a vesicle (*eph. vs.*), the thick walls of which are composed of columnar epithelium, and thus differ markedly from the folded epithelium of the anterior wall previously described. This vesicle is much flattened antero-posteriorly, its longest axis lying very nearly in the axis of the cylinder to which the epiphysis as a whole has been compared. That the structure here described is a separate vesicle, and that its cavity is not continuous with the cavity already described as a continuation of the third ventricle, admit of easy and satisfactory demonstration, not only in this particular instance, but also in all other individuals both of this species and of P. coronata of which sections have been made. In passing through the entire series of sections, it is easily seen not only that the two cavities nowhere approach more nearly to confluence than in the one represented in the figure, but also that the walls of the vesicle and those of the more proximal part of the epiphysis with which they are in relation are clearly distinct. The separateness of these two structures will appear more clearly when we come to consider the same parts in P. coronata. Passing upward and forward from the distal end of this vesicle is to be seen a bundle of connective-tissue fibres which becomes blended with the string of connective tissue already described as running from the apex of the cone to the region of the parietal vesicle. There is no indication that the epithelial wall of the epiphysial vesicle, as it may be called, passes into this string.

Covering the whole postero-dorsal convex side of the portion of the epiphysis thus far described, and even extending considerably beyond its distal extremity, is an immense blood sinus fully distended with blood corpuscles (Fig. 9, *sn. sng.*, and Fig. 8, *cp. sng.*).

Phrynosoma coronata.

1. *General Description.* — Figure 2 (Plate I.) represents a transverse section of the dorsal wall of the head, passing through the middle of the parietal eye of P. coronata. The description of the external appearance and of the vesicle and its surrounding structures given for P. Douglassii requires modification in only a few points to become applicable to this species. The depression mentioned as existing on the internal surface of the wall of the brain-case immediately under the vesicle in P. Douglassii becomes in this species a deep pit. To correspond with this pit the external surface of the wall immediately over the vesicle forms

a low, broad cone, a condition which gives quite a different general appearance to the sections in the two species. In P. coronata the vesicle is situated somewhat nearer the external surface of the cranial wall than in P. Douglassii; and the intervening connective tissue differs less, both as regards the fineness and direction of its fibres, from the adjacent tissues, than in the case of P. Douglassii. The vesicle, with its connective-tissue capsule, protrudes into the bottom of the pit considerably. The pit is bridged over by the dura mater of the brain, and thus a chamber is formed in which a great quantity of blood corpuscles is found (*cp. sng.*). It will be remembered that no such blood sinus in this region exists in P. Douglassii, but that numerous blood-vessels do occur here. In P. coronata, however, the sinus replaces the vessels.

2. *The Parietal Vesicle.* — With regard to the vesicle itself, the only points in which it differs very essentially from that found in P. Douglassii are the absence of the cavities in the retina regarded as blood-vessels, and the far less perfect development of the structures projecting from the internal surface of the retina into the cavity of the vesicle. The latter difference I am inclined to think due to the probably somewhat greater degree of degeneration of the retinal cells which secrete these structures. That this portion of the retina is more degenerated in P. coronata may be supposed from the fact that we find here considerably more pigment than in the corresponding region in P. Douglassii. However, too much stress must not be laid on the greater or less quantity of pigment, since the quantity is quite variable even within the same species. In one individual of this species pigment was found, though in small quantity, in the lens.

3. *The Epiphysis.* — Although this structure does not differ in any essential particular from what we have already seen in the preceding species, the fact that several of the points which go to make the study of the epiphysis of much interest are here well brought out, has made it seem best to describe and illustrate the organ in detail. Figures 10, 11, and 12 (Plate IV.) present vertical longitudinal sections from the same animal at different planes to the left of the median plane, Figure 12 being very nearly median, and Figure 10 farthest removed from it. It should here be said, however, that the sections are not quite vertical; so that, while the epiphysial vesicle is situated more to the left than to the right side of the sagittal plane, yet it is less so than would be inferred from the way in which it appears in the figures. The form of the epiphysis, as a whole, is nearly the same as that found in P. Douglassii, and it is composed of the same parts; — namely, a proximal

part with an anterior much-folded epithelial wall, and a posterior not folded and thinner epithelial wall; an epiphysial vesicle; a blood sinus; and a string of connective tissue extending from the distal end of the vesicle and blood sinus to the region of the parietal vesicle. In the anterior wall of the proximal portion the folding extends down somewhat nearer to the brain than is the case in P. Douglassii, and just at its junction with the brain a large blood-vessel is found filled with blood corpuscles (Fig. 12, *cp. sng.*). As already said in describing the posterior wall in P. Douglassii, the connection (opposite the letters *vnt.*^{3}) with the brain is here complete and very evident, though the roof of the third ventricle (*tct. thl. opt.*) appears in the section to constitute a part of this wall.

The cells composing the walls of the proximal part are about two or three deep, but not arranged in layers. They are small, distinctly nucleated, and the nuclei are apparently perfectly round. They stain readily. On the outer surface of this wall is found, throughout most of its extent, a very thin layer of tissue, the cells of which are much flattened. This layer becomes continued from the apex of the epiphysis as the connective-tissue string (*con't. tis.*) already mentioned as passing to the region of the eye; another portion of it also becomes continuous with the pia mater of the brain.

Figure 10 represents a section through the longest portion of the epiphysial vesicle. In this plane the proximal portion of the epiphysis has not yet appeared, and is not found till we pass to a section in which the long axis of the vesicle has become considerably shortened. In the wall of the vesicle three zones or layers are found. The external one is similar to — in fact, on the posterior surface is continuous with — the thin external layer mentioned in the proximal portion. The second zone, comprising more than half of the entire thickness of the wall, is composed of cells apparently of the same nature as those described as forming the chief portion of the wall of the proximal part; but the layer is considerably thicker here than there, and on the whole rather more compact (*e'th.*, Figs. 10 and 11). The third and most internal zone is a deeply pigmented one (*pig.*). This pigment is so dense that when destroyed no distinguishable structure remains. In the presence of this pigment the species now under consideration differs entirely from P. Douglassii, where no pigment in this region is found. Again, however, attention is called to the fact that great importance cannot be attached to the presence or absence of pigment. Figure 11 shows the relation between this vesicle and the proximal portion of the epiphysis. In this section it will be seen that a distinct line of demarcation exists between the true epithelial portions of the two walls where they come in contact. This distinctness is maintained throughout the entire series of sections. When the median section is reached, the vesicle has entirely disappeared. From the distal end of the vesicle the connective-tissue string extends forward to the region of the eye, as in the case of the proximal portion (*con't. tis.*). The blood sinus (Fig. 12) does not, in this species, come in contact with the epiphysial vesicle, but occupies the same position on the proximal part as in the case of P. Douglassii. It is much smaller in P. coronata, but in other respects is of the same nature. Whether or not this epiphysial vesicle may be homologized with the secondary vesicle in Petromyzon (Ahlborn, '83, Beard, '89, Owsjannikow, '88, Wiedersheim, '80) can be profitably discussed only after its development has been studied. So far as the condition in the adult is concerned, there is little to indicate such a homology.

I mention here an observation which may be of significance in connection with this complicated structure of the epiphysis. In both species and in all the individuals of Phrynosoma of which I have made sections favorable for exhibiting the entire dorsal surface of the brain, I have noticed that the pia mater appears to form a junction with the connective-tissue string described as passing from the distal extremity of the epiphysis to the region of the parietal eye, and also that it is thrown into several folds on the dorsal surface of the cerebellum. The membrane where folded is considerably thicker than elsewhere, contains within its folds numerous blood-vessels, and is composed of a single layer of cells very regular and distinct in outline and of a decidedly epitheloid appearance. The condition reminds one strongly of the folded portion of the wall of the epiphysis.

Uta Stansburiana.

As I have had but two specimens of this species, both preserved in alcohol, and hence not in the best histological condition, my study of it has been less satisfactory than that of the species of Phrynosoma. A few points, however, have been observed which are of some interest; but these can be presented without entering into a detailed description of the structure. Figure 6 (Plate II.) represents a portion of a sagittal section through the dorsal wall of the head and the parietal vesicle. The parietal foramen, too broad to be embraced in the figure, is much larger here than in Phrynosoma, and the vesicle can scarcely be said to be embedded in the connective tissue of the brain roof, as in the case of Phrynosoma, but rather is suspended from the under side of the wall in a connective-tissue capsule.

The most striking features about this vesicle, as seen in the section, are its dorso-ventral flattening, and the entire separation of the lens from the retina. The lens, a well defined structure, composed of much elongated, almost fibrous, non-stainable cells, has its margins widely separated from the retina, and the intervening space is occupied by a uniformly fine granular substance (*cog.?*), which also occupies the narrow space corresponding to what would be the cavity of the vesicle, were the lens and retina continuous at the margins of the former. The retina shows no structure beyond two deeply pigmented layers, corresponding to its external and internal surfaces, connected at short but irregular intervals by pillars of pigment, between which are seen a few scattered nuclei. This distinct separation of the margins of the lens from the retina is the only undoubted case of the kind, so far as I know, that has been seen, and if normal may be of significance in connection with the theory of the origin of the eye recently advanced by Beard ('89). I am, however, inclined to believe, notwithstanding the fact that the condition here found is apparently confirmed by the sections of my second specimen of this species, that the separation is in reality due to the extreme differentiation of the two structures, by means of which the connection between them was weakened, and then to artificial rupture by the flattening of the vesicle. The point certainly needs confirmation in more carefully preserved specimens.

I was unable to study the epiphysis in the material which I had, but no trace of anything like a nerve or even like a connective-tissue string extending from the parietal vesicle could be detected, nor were there any indications of blood-vessels or sinuses corresponding with those existing in Phrynosoma found here.

Conclusions.

The general bearing of the facts here presented I discuss at present only in connection with the question of the function, past and present, of the parietal organ. I concur in the opinion held by most of the persons who have written on the subject, that the organ is a degenerate eye, although my observations furnish, perhaps, no evidence in addition to what has been presented by former writers, in support of the belief. From the morphologist's point of view, the evidence that would remove all doubt as to the correctness of this opinion would be that the vesicle regarded as the eyeball should be composed of elements essentially similar to elements found *somewhere* in organs known to perform the mechanical part in the act of vision; and, second, that this vesicle should be connected with the brain by a nerve comparable with the optic nerve of *some known* functional eye. I think no one familiar with the structure of the vesicle as it exists in many Lacertilia and in Petromyzon, will refuse to accept as satisfactory the evidence on the first point. The evidence on the second point is less conclusive. In many cases where the vesicle is well developed, as in Phrynosoma, it is certain that nothing which can be justly compared to an optic nerve exists. Spencer ('86 and '87) and several succeeding writers have held it as beyond doubt that in several species, notably of the genera Lacerta, Hatteria, and Varanus, there is a nervous connection between the brain and vesicle. Leydig ('89), however, in his preliminary, based on his study of Lacerta ocellata, Varanus elegans, and other forms, says "der von Spencer beschriebene Nerv ist kein Nerv sondern das strangartig ausgehende Ende der Zirbel." Lacerta ocellata is one of the forms in which Spencer ascribes, with least question, a nervous nature to the structure under consideration; but apparently Leydig has not examined either of the species of Varanus, viz. gigantea and Bengalensis, which Spencer studied; while, on the other hand, V. elegans, Leydig's species, is not mentioned by Spencer as having been studied by him. This denial *in toto* of the existence of the nerve as described by Spencer, Leydig practically repeats in his most recent contribution to the subject (Leydig, '90), and adds, as further confirmation of his opinion, that he has studied Hatteria (he does not tell us what species) and finds that here also the so-called nerve is of the nature of connective tissue. He also comes to the conclusion in this communication, that, while from the structure of the vesicle alone the organ must at least be put among the sense organs, it is yet "as good as impossible to do so while it is recognized that in the parietal structure of all the animals investigated by me not one contains a nerve, for we must hold fast to the proposition that for the equipment of a sense organ the peripheral end of a nerve is necessary." It appears to me, however, that we are not compelled to relinquish the belief that the organ was originally an eye, even though we accept Leydig's statement, as against Spencer's and others, regarding the nature of the supposed nerve in the cases which both have examined; or even should it appear that in no case does the nervous connection *now* exist.

It seems to me that Leydig has not given sufficient prominence to the possibility, not to say great probability, that the nervous connection has been lost by the modification and degeneration which the whole structure has certainly undergone; and especially must we hesitate in rejecting this explanation, when we remember that by so doing we are compelled to seek another. To be obliged to ascribe a function other than that of vision to a structure entirely like an organ of vision in most of its essential parts, and differing widely from one in no essential point, is requiring us to accept a conclusion that would throw suspicion on all our morphological reasoning. Should it be shown conclusively that the vesicle never has, in any vertebrate, *either in the adult* or *during its ontogeny*, nervous connection with the brain, then we should be obliged to abandon the optical explanation of its origin, and turn to the exceedingly difficult task of finding another. But until such knowledge is at hand, it seems to me we must suppose that the organ was produced as an eye, that in some way entirely unknown to us it lost its optical function, and that, in the consequent modification and degeneration, the optic nerve degenerated more rapidly in some cases than did the optic vesicle; and that in this way the separation which we now find took place.[1]

In previous discussions of the nature and function of the parietal organ, I believe sufficient attention has not been given to the structure and development of the epiphysis and its relation to the parietal vesicle, and especially its relation to the so-called choroid plexus. I have designated the entire structure found in connection with the roof of the thalamencephalon as the epiphysis; but, as already said, I have considerable doubt as to the wisdom of so doing. For the sake of precision it would seem best that the term epiphysis should be limited to the structure which arises as an evagination from this portion of the brain. Certain it is that the large blood sinus which I have described as a part of the epiphysis in Phrynosoma cannot be regarded as forming an essential portion of the structure, and I think it quite possible that what I have called the epiphysial vesicle is not a portion of the epiphysis, should the term be limited as I have suggested that it ought to be. The distinctness of the epiphysial vesicle from the proximal portion of the epiphysis in the adult Phrynosoma is without exception, so far as my observations have gone; and if it is regarded as having been derived from the epiphysis, then we have two vesicles instead of one that have arisen in this way, and the difficulty of explaining the nature and function of the whole structure is correspondingly increased.

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[1] Concerning the nervous connection between the eye and the epiphysis in Anguis fragilis, Strahl and Martin say ('88, p. 154), "Der Nerv der nach hinten am Vorderrand der Epiphyse scheinbar verschwindet, tritt von unten her in das Auge ein." Francotte ('88, p. 782) also describes essentially the same condition in this species. But such a condition would be so anomalous that C. K. Hoffmann ('88, p. 1991), notwithstanding the agreement of these independent statements, has, it seems to me with reason, expressed doubt as to the trustworthiness of the observations.

In his recent paper, Leydig ('90) has expressed the belief that there are two forms of parietal organs. He says: "From the posterior portion of the embryonic thalamencephalon (Zwischenhirn), especially in Lacerta agilis, two thick-walled vesicles (Blasen) bud out just in the middle line, lying one behind the other and springing from a common root (einem Wurzelpunkte). The anterior vesicle gives rise to the parietal organ, and the posterior one constitutes the epiphysis (Zirbel)." It is only, he says, from the anterior of these two vesicles (Blasen) that a vesicle (Blase) becomes cut off, and attains an eye-like character; the posterior one ends in the expanded blind terminal portion of the epiphysial thread (Zirbelfaden). But Selenka ('90) informs us, in a still more recent communication, that, after studying the development of the brain in a large number of reptiles and other vertebrates, he is unable to confirm Leydig's statement as to the origin of the parietal eye. He does find, however, in all cases, an evagination from the dorsal wall of the *fore* brain very similar to the one that forms the epiphysis from the roof of the thalamencephalon; also that the two structures elongate *pari passu*, the epiphysis becoming directed upward and forward, while the anterior evagination, which he calls the "paraphysis," becomes directed upward and backward. After the parietal vesicle is cut off from the epiphysis, the distal end of the paraphysis grows in between the vesicle and the end of the epiphysis from which it was detached, and the vesicle comes to lie on the paraphysis as on a pillow.

The relation of the two structures in the adult he does not know. C. K. Hoffmann ('85) has also described an evagination from the roof of the brain at the place of transition from the fore brain to the thalamus, which he calls the ependyma, — the beginning of the choroid plexus, — and he says that in the grown animal "it comes to take a not inconsiderable part in the formation of the epiphysis." Although there is nothing in the brief papers of either Leydig or Selenka to indicate whether or not the additional more anterior evagination seen by them is the same as that described by Hoffmann, yet, since all have studied the same forms, viz. of the genus Lacerta, it seems quite probable that they have all observed the same structure. Whether or not any portion of the epiphysis as I have found it in Phrynosoma corresponds to the paraphysis of Selenka, or the ependyma of Hoffmann, can of course be determined only by studying the development of this portion of the brain.

Bearing in mind the highly vascular condition of all parts of the parietal organ, the numerous large blood-vessels surrounding the vesicle in P. Douglassii, and the great sinus in the same region in P. coronata, the sinuses of the epiphysis in both species, as well as the great quantity of blood contained in the much folded anterior wall of the epiphysis, it seems to me impossible to escape the belief that, in this genus at least, the organ must have some physiological significance. Leydig ('89) has expressed the opinion that it belongs primarily to the lymph system. From what has already been said, it is evident that I cannot accept this conclusion; but it does appear to me highly probable that the structure has become secondarily of such a character. From the numerous instances of change of function in the animal organism to which attention has been directed by Dohrn ('75), Kleinenberg ('86), Lankester ('80), Weismann ('86), and others, there are certainly no *a priori* objections to such a view, and it seems to afford more nearly a satisfactory explanation of the present condition of the organ than does any other.

CAMBRIDGE, August 15, 1890.

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EXPLANATION OF FIGURES.

All the figures are camera drawings excepting where otherwise indicated in the explanations.

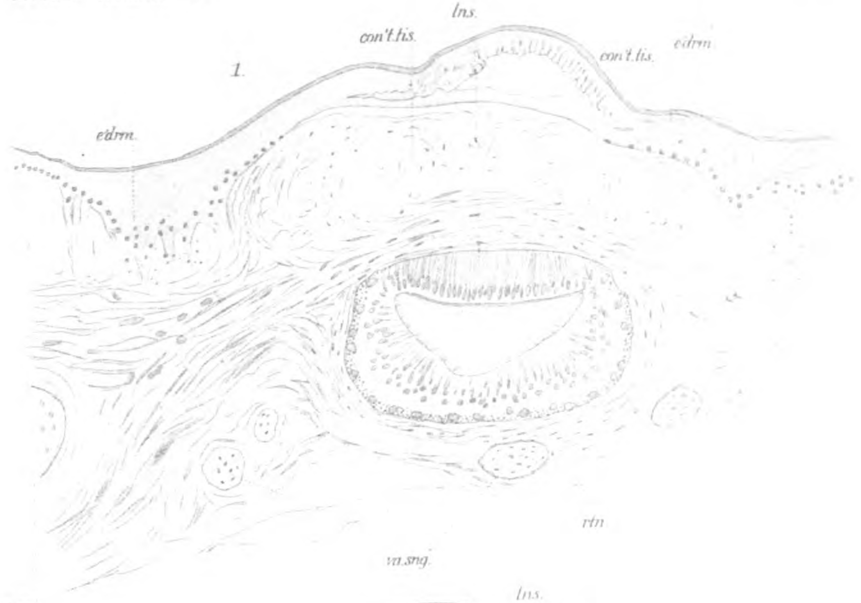
ABBREVIATIONS.

cav. e'phy.	Cavity of the epiphysis.
cbl.	Cerebellum.
ceb.	Cerebrum.
chs. opt.	Optic chiasm.
cl. i.	Cells of zone 5 of the retina.
cl. lns.	Cells of the lens.
cog.	Coagulum.
com. a.	Anterior commissure.
com. p.	Posterior commissure.
com. su.	Superior commissure.
con't. tis.	Connective tissue.
cp. sng.	Blood corpuscles.
e'drm.	Ectoderm.
en'th. va.	Endothelium of retinal blood-vessels.
eph. vs.	Epithelium of the epiphysial vesicle.
e'th.	Epithelium.
la. trm.	Lamina terminalis.
lns	Lens
lob. opt.	Optic lobes.
m. scu.	Scale of the parietal eye.
mac. opt.	Spot marking the position of the parietal organ.
mb. ba. ex.	External basement membrane.
mb. ba. i.	Internal basement membrane.
nl.	Nucleus.
nl′.	Nuclei of zone 2 of retina.
nl″.	Nuclei of zone 4 of retina.
nl‴.	Nuclei of zone 5 of retina.
os par.	Parietal bone.
pig.	Pigment.
prc. r.	Processes radiating from the external basement membrane.
rtn.	Retina.
sn. sng.	Blood sinus.
tct. thl. opt.	Roof of the optic thalamus.
thl. opt.	Optic thalamus.
va. rtn.	Retinal blood-vessels.
vnt.^{3}	Third ventricle of brain.
vs.	Epiphysial vesicle.
z″.	Second zone of retina.

PLATE IV.

Figs. 10, 11, 12. The left faces of three sections of *P. coronata*, parallel with the sagittal plane, — Figure 12 nearly median, Figures 10 and 11 to the left of it. Figure 10, farther to the left of the median plane than Figure 11, passes through the longest part of the epiphysial vesicle. Figure 12 is more highly magnified, to show the histological structure. Figs. 10 and 11 × 40. Fig. 12 × 90.

1.



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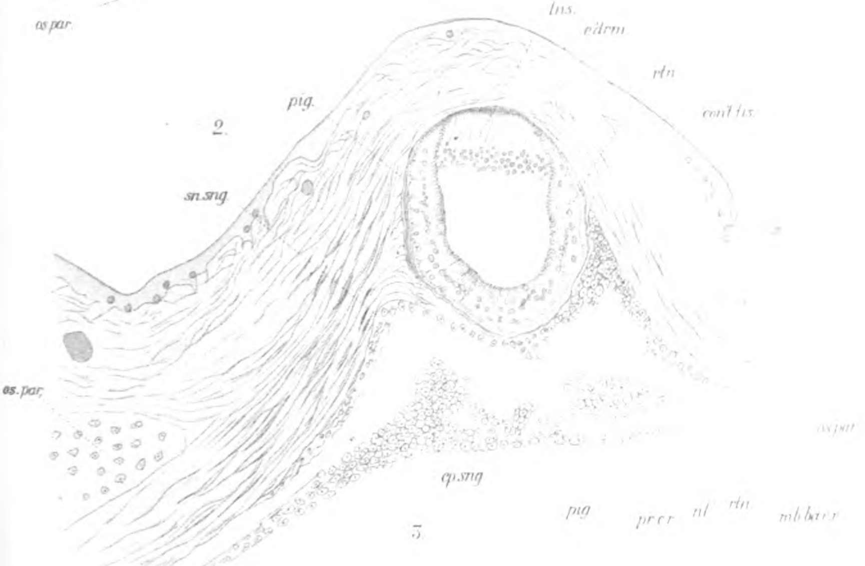

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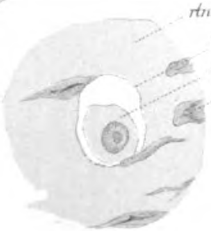

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XXI.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE.

XXIII. — PRELIMINARY NOTICE ON BUDDING IN BRYOZOA.

By C. B. Davenport.

Presented February 11, 1891, by E. L. Mark.

Since several months must elapse before the publication of my studies on Budding in Bryozoa, it has been thought best to present, in a preliminary communication, some of the more important facts gained.

In my paper on *Cristatella*,* I described for that genus a mass of cells lying between the ectoderm and muscularis which gave rise, by active cell proliferation at certain regions, to the inner layer of the polypide, — the layer from which the inner lining of the kamptoderm, the outer layer of the tentacles, the nervous system, and the digestive epithelium arise. This inner layer has been brought into prominence by the conceptions of Hatschek concerning its significance, — conceptions which appear to have influenced some of his followers in their study of marine Bryozoa. According to Hatschek, this inner layer is to be regarded as entodermic in origin, and to give rise to the digestive epithelium only. The latter part of this view is certainly incorrect, as shown by the concurrent testimony of Braem and myself. It remained, however, to determine the *origin* of the layer, or rather of the stolonic mass from which it arises. The "stolonic mass" arises in the embryo, soon after the completion of the two-layered condition, from the ectoderm, at the same pole as that at which the so-called gastrulation takes place. A disk of cells sinks below the general level of the ectoderm and becomes overgrown by that layer. This disk expands rapidly at the base of the ectoderm, and in all directions of the plane, by cell proliferation, and gives rise to the first polypides. The first two polypides, one of which is slightly older than the other, arise so that their anal surfaces are turned towards each other.

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* Cristatella: the Origin and Development of the Individual in the Colony. Bull of the Museum of Comp. Zoöl. at Harvard College, Vol. XX, No. 4, November, 1890.

The cœlomic epithelium arises by a sort of ingression, as observed by Korotneff, and is to be regarded, probably, as mesoderm plus entoderm, the entoderm being reduced to a still more rudimentary condition than in Gymnolæmata.

In *Plumatella*, the inner layer of the primary polypide arises near the pole of ingression directly from the outer layer of the two-layered sac, and not from a mass which has already lost its connection with the outer layer, as in Cristatella. The second polypide arises at some distance from and wholly independently of the first, and, like it, by an invagination of the body-wall near the pole of ingression. The remainder of the polypides are derived from the indifferent cells about and in the neck of these two primary ones.

The method of origin of the primary polypides is fundamentally the same in both genera, but the conditions in Plumatella are to be regarded as the more primitive. In both, the inner layer of the polypide is derived from the neutral region of the outer larval layer whence the inner larval layer has arisen. Possibly this region should be regarded as neither ectoderm nor entoderm, but as still indifferent, and capable of giving rise to either.

The origin of the primary bud in Gymnolæmata also is probably to be referred to the pole of ingression or invagination, but owing to greater difficulties of orientation this cannot be determined so easily as in Phylactolæmata.

My studies on and drawings of *Paludicella* were already nearly completed when I first saw Braem's "Untersuchungen über die Bryozoen des süssen Wassers," in Bibliotheca Zoologica, Heft VI., 1891. With great keenness, he has been able, even by the study of the living animal, to correct some errors of previous authors, and he has anticipated some of my observations.

Each young polypide arises in the adult colony independently of any older polypide, from a mass of embryonic, rapidly dividing tissue at the tip of the branch, and some of this tissue is left behind as the tip moves forward. Typically, three masses of such tissue are left behind, at intervals corresponding to the joints of the branch. Of these three masses, one, the median, gives rise directly to the youngest polypide of the ancestral branch. The other two lie about 90° to the right and left of the median bud, and remain in a quiescent state until the median bud has attained a considerable size. The cells of these lateral masses are always distinguishable from those of the adjacent body-wall by their cuboid form. They finally give rise to lateral branches, in which polypides are secondarily developed.

Braem has offered the ingenious hypothesis that the tip of the branch is to be regarded as having been occupied, ancestrally, by a polypide which has cœnogenetically disappeared. Young polypides are on this assumption derived from the neck of older ones, as in Phylactolæmata. This hypothesis is rendered less necessary, if one conceives that in the budding process the younger bud is not derived from the older, but that *they are successively derived from the same mass of embryonic tissue*, — a view which I have already maintained concerning Phylactolæmata. *The tip of the branch is*, to my mind, *to be regarded as a stolon in both the median and lateral branches.* To form the *polypide*, the two layers of the embryonic mass of the wall are, in Paludicella, invaginated into the cœlom. But some of the cells remain in their indifferent condition as the neck of the polypide.

As Braem saw in the living animal, and as my sections and reconstructions sufficiently demonstrate, the hinder part of the alimentary tract arises in a manner comparable with that in Phylactolæmata, and its formation progresses from the anal towards the oral end. The œsophagus arises independently, and later the two pockets fuse to form the completed alimentary tract. The tentacles arise somewhat differently from those of Phylactolæmata, and in the manner recently described by Seeliger for Bugula, and they as well as the kamptoderm are here two-layered. They lie at first in two parallel rows of seven each. The anus is not removed outside the tentacular corona until the two posterior free ends of the ring canal meet and become confluent between mouth and anus. An odd tentacle, younger than the others, often arises directly oralwards of the anus. The brain arises as in Cristatella, and sends out two large circumœsophageal processes to form the commissure. The so-called *epistome* of Korotneff, Nitsche, and Seeliger, which they have believed to exist in the early stages of different Gymnolæmata, is merely the fold separating the brain cavity from the œsophagus, and has no relation to the epistome of Phylactolæmata or Endoprocta. I have found no trace of a true epistome at any stage. The body-wall is invaginated at the neck of the polypide, and the latter extends as a long cylinder for some distance below the general surface. It secretes the chitinous rods and cuticula of the adult "neck." The "collare setosum" appears to split off from the thick cuticula of the neck as a delicate chitinous cylinder, which has its distal end free and its proximal end embedded in the cells of the neck immediately around the atrial opening. From its method of origin and structure, one finds it difficult to concur with the suggestion of Professor Ehlers, that the collare setosum of Ctenostomata is homologous with the cirri of Endoprocta. Muscles and funiculi both arise from the cells of the cœlomic epithelium. The communication plates arise as a circular fold of the body-wall. The cells of the cœlomic epithelium which immediately surround the central pole become metamorphosed at their inner ends to form the teeth of the central sieve.

The polypides of the *Bicellariidæ*, *Membraniporidæ*, and *Alcyonidiidæ* arise in a similar manner to those of Paludicella; that is, from a mass of indifferent cells at the margin of the colony, — a mass from which the body-wall also is derived. The polypide arises in all cases by an invagination of the body-wall, which is two-layered at the margin of the colony. In all cases studied, the whole of the polypide is derived from this one rudiment. The alimentary tract arises, at least in some cases, exactly as in Paludicella. The ganglion arises from the inner layer of the bud, by an evagination of the floor of the atrium in both Ctenostomata and Cheilostomata, and I have found no trace of a genuine epistome at any stage.

Budding in marine Gymnolæmata seems to occur in accordance with certain laws, which may be deduced from a study of erect colonies like *Bugula*. In Bugula turrita, Verrill, we have a colony with an erect axis and branches whose points of insertion lie in a right or left handed spiral. The phyllotactic arrangement of the branches is not an invariable one, but is approximately ⅜. Each branch is fan-shaped, the handle being the point of attachment, and is slightly concave toward the axis, like the thread of an Archimedean screw. The fans at the base of the colony are largest and oldest, at the tip youngest. The individuals are arranged end to end, in lines which spring from the single most proximal individual, and increase in number as upon this and the successively more distal individuals lateral as well as terminal buds arise. Sometimes, however, but one new bud — a terminal one — arises. The branches are not wholly separate from each other, but cling together in pairs.

The following laws of growth have been deduced: — 1. The individuals "break joints." 2. The lateral buds are formed earlier, and do not extend so far distally as the terminal buds. 3. When a terminal and lateral bud attached to the same proximal individual are each immediately followed by two buds, the two lateral buds lie adjacent, the two terminals outside. 4. Lateral buds tend to arise at the same time on two branches which spring from a common individual. 5 Law 4 is modified by a superior one, according to which lateral buds arise more frequently at the edges of the fans than elsewhere. 6. The marginal branches are shortest, the middle ones longest. 7. There is one proximal individual to each "fan." This is followed by two, and these by four, of which four the two inner adjacent are lateral, the two outside ones terminal. Then each of the two outside individuals of these four bears more individuals, counting all which are formed between it and the periphery, than does each of the inner individuals. 8. New individuals are constantly being formed at the periphery of the fan, and at about the same time, but on some branches only one new bud arises, on others two. The tendency to give rise to two buds decreases as the fan grows older; and if a number of arcs be struck across an accurate drawing of an entire fan, with the proximal individual as a centre and with different radii, it will be found that the number of individuals cut by any linear unit of arc is the same for all radii.

In Bugula flabellata the fans are not attached to an erect axis, but are each attached to the rock or woodwork by their proximal individual. Three or five branches are united together, instead of two, as in B. turrita. The above "laws" are equally applicable to this species, except that No. 4 does not apply well here, being masked by another, namely, that of the three or five branches which are united together the outer ones only give rise to lateral buds. The above rules hold for *Crisia eburnea* also, which rises erect like Bugula, and has its branches united in pairs.

In genera which, like Membranipora, Lepralia, and Escharella, form creeping colonies in which all of the branches cling together, the normal architecture of the colony is obscured by inequalities of the surface upon which it lies. But under favorable conditions there is a tendency to conform to the laws which we discover in Bugula.

Regeneration of polypides has been studied in Escharella and Flustra. In these cases regeneration occurs at one point only; namely, on the operculum immediately behind, i. e. proximad of the atrial opening. Regenerated buds thus arise in the immediate vicinity of older ones, and from those cells some of which went to form that older polypide. They are formed by an invagination of the body-wall exactly as are the old polypides. Although the cells of the operculum have lost their cuboid form, and only return to it again in giving rise to the new bud, yet the nuclei appear to remain more abundant here than elsewhere on the body-wall, and this may perhaps be considered a condition of less extensive differentiation than obtains in all other parts of the body-wall.

CAMBRIDGE, February 9, 1891.

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CONTRIBUTIONS TO THE MORPHOLOGY OF THE TURBELLARIA.

I. ON THE STRUCTURE OF PHAGOCATA GRACILIS, LEIDY.

BY W. M. WOODWORTH.

WITH FOUR PLATES.

CAMBRIDGE, U.S.A.:
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No. 1. — *Contributions to the Morphology of the Turbellaria.* — I. *On the Structure of Phagocata gracilis, Leidy.* By W. M. Woodworth.[1]

In the fall of 1887, Mr. H E. Valentine of West Somerville, Mass., brought to the Embryological Laboratory of Harvard College some planarians, with the suggestion that they might be infested with parasites. The planarian proved to be the interesting Phagocata gracilis of Leidy, and the supposed parasites were the pharynges of the complicated digestive apparatus. At the suggestion of my instructor, Dr. E. L. Mark, I undertook the study of this curious Triclad.

The animal, which was afterwards named by Leidy Phagocata gracilis, was first described by S. S. Haldeman ('40, p. 3) in 1840, under the name of Planaria gracilis: "Body oblong, suddenly tapering to a point posteriorly: sides nearly parallel; head square in front, with a projecting appendage on each side: neck narrowed; eyes (two) situated on each side of the narrower part; these are oblong and white, with a black dot at their internal side: ventral opening less than one third the entire length from the posterior extremity, and from this opening an intestine is sometimes protruded. General color fuliginous, veined with black. Length, $\frac{3}{4}$ in., breadth, $\frac{1}{10}$. Hab. springs in Eastern Pennsylvania."

In 1848, Leidy published a further description of the species, giving to it the name of Phagocata ('48, p. 248), because, as he says, "I detected such a remarkable peculiarity in the digestive apparatus as led me to investigate its anatomy in detail, and to form for it a separate sub-genus, characterized as follows: —

"*Phagocata*, oblonga, plano-convexa, nuda, contractilis, mucosa, antica auricularia. Aperturæ duæ, ventrales, ad os et ad generationem pertinens. Proboscides multæ.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXIV.

No. XXIII. of these Contributions appeared in the Proceedings of the American Academy of Arts and Sciences, Vol. XXV., under the title, "Preliminary Notice on Budding in Bryozoa." By C. B. Davenport.

"*P. gracilis*, nigricans, lateribus parallelis, postero acuto abrupte, plerumque antico recto; oculis duobus. Long. 9 lin., lat. 1 lin. Habitat in fontis Pennsylvaniæ.

"*Description.* Oblong, limaceform, naked, convex superiorly, flat inferiorly, very contractile; sides ordinarily parallel, convex when the animal is in a contracted state, convergent anteriorly when elongated; anterior extremity with a lateral triangular auricular appendage, straight in front, by contraction becoming convex or concave; posterior extremity abruptly pointed; ocelli two, anterior, composed of an oblong, semi-transparent (nervous?) mass with an intensely black dot of pigmentum at the internal posterior part; ventral apertures two; oral aperture a little less than one third the length of the body from the posterior extremity. Color black or iron gray, and in some younger specimens latericeous."

I have quoted Leidy's description in full, because it seems to me that the first description of so striking and aberrant a species is of uncommon interest.

It is noteworthy, that, notwithstanding the faithfulness of the description, and the remarkable peculiarities of the worm, no mention of the species has been made for over forty years. It is also strange that Girard should have been ignorant of the existence of Leidy's paper, for in his list of North American fresh-water Planariæ ('51, p. 264) he uses the name proposed by Haldeman, "Planaria gracilis," and says that it is "common about Cambridge in pools and rivulets." He adds, in a note, "Planaria gracilis and very likely Planaria tigrina will not remain in the genus Planaria as soon as we shall know their internal structure." In a subsequent paper ('51ᵃ, p. 2), "Die Planarien und Nemertinen Nord-Amerikas," the species is described under the name given to it by Leidy, but no mention is made of the most striking characteristic discovered by that observer, — the multiplicity of the pharynges.

The structural peculiarities of Phagocata were not simply ignored, they were even denied by no less an authority than von Siebold, who explained the "proboscides" of Leidy as so many processes from the lip of one normal pharynx. After quoting the description, he says ('50, p. 389): "Das erwachsene Thier soll 23 Rüssel haben, die es beim Fressen alle hervorstreckt; Ref. vermuthet, dass der Rüssel eine trichterförmige ausgezackte Mündung besitzt, und dass die beweglichen Fortsätze des Rüsselrandes für ebenso viele einzelne Rüssel gehalten worden sind."

Diesing, like von Siebold, was incredulous; in his "System," he says ('50, p. 207), "Œsophagus protractilis multi partitus (proboscides multæ Leidy)." Twelve years later, in the "Revision der Turbellarien," he writes ('62, p. 506), "œsophago multipartito."

Stimpson ('58, p. 23) in his Prodromus apparently followed Diesing, for he says "œsophago protractili multipartito."

Recently, Professor Leidy ('85, p. 49) has figured Phagocata gracilis in a popular account of "Planarians." These are the only descriptions of Phagocata I have been able to find.

Phagocata gracilis, Leidy.

When viewed from above, the general form of the animal is elongated; its lateral margins are nearly parallel, being slightly convex posteriorly; the widest part of the body is in the pharyngeal region. The largest specimens measure 30 mm. in length by 4½ mm. in breadth. Anteriorly the sides converge slightly up to about the region of the eyes, where the diameter increases, thus forming the so called head. This bears the lateral auriculate appendages. The lateral appendages are rounded, rather than triangular as described by Leidy; they are continuous with, and in fact form part of, the anterior extremity; posteriorly, the sides converge to a point (Fig. 20 *a*). The eyes appear as two elongated oval white spots, with black pigment on the internal edge. They are situated on the narrow part or "neck."

Haldeman and Leidy have described the head as being "straight in front." This appearance is seen only when the animal is at rest. It is then much contracted in the direction of its antero-posterior axis, and is usually much distorted; at such times it often appears as a shapeless black lump, this condition probably being a means of protection (Figs. 20 *b* and 20 *c*). When in motion the anterior extremity is usually convex, but not always, for it may be straight, sinuous, or concave; these shapes are only temporary, following each other in quick succession. The head changes its form especially when the animal approaches some object; for this part of the body is functional as an organ of touch; that it is suited structurally to be a kind of feeler will be evident from the description of the nervous system which follows.

Phagocata gracilis has a shiny black appearance when viewed by reflected light, but by transmitted light it is of a greenish gray color. The color may vary from black to a reddish brown on the one hand, or to a light gray on the other. I have seen small specimens which were almost milky white. The ventral surface is of lighter color than the dorsal, and there are light areas about the ventral apertures. The pigment is densest in the dorsal median line, where it forms a dark band; it diminishes toward the sides of the animal, the edges of which are quite destitute of it. The distribution of the pigment in the head region presents many variations. In most cases the posterior borders of the auriculate appendages show two light spots, and there is a third one, somewhat triangular in shape, at the anterior end in the middle line. The marginal area of the head, like that of the body, is free from pigment. Sometimes the whole head region is light with the exception of the middle line between the eye spots, where there is an extension of the dark median band previously referred to. Light non-pigmented areas occur wherever there has been a reparation of the tissues resulting from injury.

By an examination of the animal in the natural condition, only a few of the internal structures can be identified, because of the large amount of pigment present. When viewed from above, the most striking feature is a large oblong light region, the pharyngeal cavity with its contained pharynges. Immediately behind this a similar but smaller spot marks the position of the penis. From the ventral side the nervous system may be dimly seen as two long whitish bands united by transverse commissures and coming together in the head region in a bilobed enlargement, the brain. Leidy apparently confused these structures with the excretory organs, no trace of which can be seen on the living animal. He says ('48, p. 250): "There appears to be nothing peculiar about the arrangement of the blood-vessels, if such they be: the term being applied to two semi-transparent lines passing along each side of the ventral surface, and a third along the middle of the dorsal surface, the three freely communicating with each other by transverse lines and numerous smaller branches, the whole forming an extensive reticulation upon the surface of the body. At the anterior part of each ventral line, I distinctly observed a dilatation to exist." And again: "I could detect no traces of a nervous system." The two "semi-transparent lines" are without doubt the longitudinal nerve trunks, and the "dilatations at the anterior part of each," the lateral enlargements of the brain. What he means by the "third" line "along the dorsal surface," I cannot say. When sexually mature individuals are subjected to pressure, parts of the vasa deferentia and oviducts can also be made out.

Phagocata differs from all other Triclads in possessing many pharyngeal tubes instead of one. All the pharynges lie in a common chamber, and when protruded reach the exterior through a single orifice, but they open into the intestinal cavity separately. One of these pharynges, like the single pharynx of other Triclads, joins the intestine at the junction of its main trunks; the others are connected with the inferior median surface of the lateral trunks (Plate II. Fig. 20). The odd median pharynx is largest, and therefore most prominent of all. The others, which arise from the intestine farther back, are successively shorter, as well as narrower, the more remote they are from the median proboscis. The attachment of the smallest ones is about as far from the posterior end of the animal as the attachment of the chief one is from its anterior end, so that the chamber which they all occupy embraces the middle half of the body. Although there are about as many pharynges attached to one of the lateral trunks of the intestine as to the other, they are not arranged in pairs, nor have their positions any definite relation to the side branches of the intestine which open into the lateral trunks. The pharynges are rather less numerous than the side branches; they sometimes arise opposite to a branch, sometimes opposite to a space midway between two branches, or at other intermediate points. The foremost of the lateral pharynges is often considerably in advance of the corresponding proboscis of the opposite side of the body (Fig. 20). Leidy ('48, p. 249) has well described the appearance and action of the pharynges in the living animal. He says: "They are considerably longer, but narrower, than in *P. lactea*, and when not in use are packed together within the animal, so that, when the latter is placed beneath the microscope and slightly compressed, they will be seen pressing upon one another in such a manner that, if one changes its position, it will be instantly occupied by another. Those which are formed last are smallest, but they soon gain their full size. If one of these animals be punctured or cut, one or more of the proboscides will be instantly protruded as if they existed under pressure, and will move about in all directions, appearing as if entirely without the control of the animal; or if one of the animals be crushed between two slips of glass so that the proboscides will be torn from their attachment, they move about involuntarily, always in a line forwards or towards the mouth. . . . In this progressive course they constantly contract and dilate; the mouth opens, and any matter in its vicinity rushes in, when it is closed and the matter passes onwards, and by the alternate contraction and dilatation of different parts of the same tube it is thrown backwards and forwards several times, and finally violently expelled at the torn extremity. When they have escaped from the ruptures of the tegument produced by crushing, or when snipped off with a pair of scissors whilst the animal is feeding, they will present the same curious phenomena. In fact, these curious independent movements caused me at first to mistake the organs for viviparous young, and it was not until I had frequently observed the animal feeding, and examined its structure beneath the microscope, after having fed them upon colored food, that I was convinced of their true nature."

It was these automatic movements of the detached pharynges that at first led me also to believe that they were parasites. They appear as long, white worm-like bodies, one end being truncated, the other ragged and uneven, where it was torn from its attachment. They move about quite rapidly by means of the cilia with which they are covered, and waves of contraction continually pass along the length of the tube from the truncated to the ragged end. The mouth end may be greatly expanded so as to form a funnel-like structure, or it may be so contracted as to obliterate the lumen. I did not succeed in satisfying myself of the real nature of these structures until I examined one of the animals while it was feeding. I placed one of the Lumbriculidæ in a watch-glass with a Phagocata, which soon attached itself to the annelid by throwing out its many pharynges, some of which were wrapped about the victim, while others were thrust into its body (Plate II. Fig. 13). The soft parts of the prey were rapidly sucked up and swallowed by means of the peristaltic motions of the pharynges, so that in a short time there was left nothing but the empty and shrivelled integument.

By far the best reagent for killing is hot corrosive sublimate. An excess of the salt is added to the saturated aqueous solution and the whole is heated to the boiling point. A very strong solution can be prepared in this way, as the salt is more soluble in hot water than in cold. Kennel ('88, p. 455) has recommended the use of 50% nitric acid. I have used with entire success a modification of his method, viz. a cold saturated solution of corrosive sublimate in 50% nitric acid. The worm is placed on a plate in as little water as possible, and when properly extended the fluid is quickly poured over it. After a few minutes' immersion the fluid is replaced by a saturated aqueous solution of corrosive sublimate, in which the worms remain for half an hour and are then washed. I know of nothing else that will kill so quickly, and at the same time leave the tissues uninjured. For the study of the intestinal tract, unstained specimens were cleared in clove oil. The amount of pigment so obscures the organs lying beneath, that the ramifications of the intestine could be traced only on cleared specimens in which the intestine contained dark-colored food matter. For staining, Grenacher's alcoholic borax carmine followed by differentiation with acid alcohol proved to be the most useful and reliable method. I have stained both *in toto* and on the slide. Good sections for topographical study were obtained by staining in alcoholic borax carmine for 24 hours and cutting in the horizontal plane sections 30 μ in thickness. By thus lightly staining, the nerve tissue takes none of the color, and in such comparatively thick sections the finer branches show as white lines against a red background. Orth's picrocarminate of lithium is a valuable reagent on account of the selective action of the picric acid for all glandular tissue, which it brings out in sharp contrast to the red color of the other tissues. I have used this reagent also with excellent results for macerating. The affinity of hæmatoxylin stains for formed substances renders them of little use; their intense reaction with the great number of glandular structures tends to obscure results. For isolation preparations, the best results were obtained by macerating directly in the stain. I also used successfully the osmic-acetic method of maceration on fresh material. The isolated living pharynges were killed in hot 1% silver nitrate for the purpose of demonstrating the epithelium. Depigmenting was accomplished by the use of a 1% solution of potassic hydrate which was allowed to act for a few minutes on sections fixed to the slide with Schällibaum's clove-oil collodion fixative.

Cilia are present over the whole surface of the animal. In material that had been prepared in hot corrosive sublimate, the middle region of the ventral surface, where the hypodermis is thinnest, was often destitute of cilia. Likewise at the lateral edges they may be wanting. These conditions are, however, due to the action of the reagent, since in the living animal cilia are always present in these places. At the anterior end of the body on either side of the head, the cilia are somewhat longer than elsewhere. They attain their greatest length at that portion of the margin of the head which forms the auriculate projections. From the middle of each projection they gradually diminish in length until, at the anterior tip of the body and at an equally distant point behind the auricles, they are reduced to the normal length. These two areas covered by the longer cilia probably correspond to the "Tastorgane" of Iijima ('84, p. 366), and are directly related to local modifications of the hypodermis.

I cannot find either the short immovable hairs or the long "Geisselhaare" seen by Iijima in other Triclads at the anterior margin midway between the areas of the "Tastorgane"; nor have I found in Phagocata that the cilia in the head region move in different directions, as Minot ('77, p. 407) has observed in the case of other fresh-water planarians.

There has been a difference of opinion among writers as to the possibility of certain regions of the body being normally destitute of cilia. Metschnikow ('66, p. 436) and Kennel ('79, p. 125) found cilia covering the whole surface in Rhynchodesmus and Geodesmus, but Zacharias ('88, p. 542) states that the dorsal surface of a variety of Geodesmus is bare, and Vejdovsky ('90, p. 132) maintains the same for Microplana, the cilia in the latter cases being confined to the ventral surface or sole. It seems to me, however, that Moseley ('74, p. 118) long ago offered a satisfactory explanation of the condition, by saying that in Bipalium the cilia on the dorsal surface of land planarians, being weaker through comparative lack of function, are consequently more easily destroyed by the action of the reagents used in the preparation of the material. Considering the habits of land planarians, and especially the dissimilar conditions to which the dorsal and ventral surfaces are subjected in regard to moisture, exposure, contact, etc., it is not strange that the conditions of the cilia of the different surfaces should be unlike. Iijima ('84, p. 366) states that it is the exception for the edges of Dendrocœlum lacteum to be ciliated, and that the almost constant absence of cilia is due to certain parasites (Trichodina). He also speaks of a species of Geoplana from South America in which the cilia of the dorsum are replaced by a granular crust. I believe that in planarians there is primarily no localization of the cilia, and that all non-ciliate conditions are secondary.

I could nowhere find a *cuticula.* The superficial portion of the cells of the hypodermis takes a somewhat deeper stain than the body of the cells, but there is no sharp line of demarcation between the two; the color of the superficial portion fades gradually into that of the body of the cell. A true cuticula such as that described by Minot ('77, p. 407) and Loman ('87, p. 69) for Triclads, and by Keferstein ('68, p. 16) for Eurylepta, is wanting, and there is only a thickening, a condensation, of the superficial plasma of the hypodermal cells.

The *hypodermis* has proved to be the most difficult of the tissues to study, because of the minuteness of its elements, and the enormous number of dermal rods, or rhabditi, which so obscure the true conditions that it is only after long and patient study of thin sections and of macerated material that one can learn what the true characters of this tissue are.

The hypodermis is thickest on the dorsal surface; it becomes thinner toward the edges of the body, and in passing around to the ventral surface it still continues to become thinner as far as the middle line, where, forming part of the floor of the pharyngeal cavity, it reaches its greatest attenuation. There are hypodermal thickenings around the oral and genital openings, and also over two sensory areas on the ventral surface of the head region, which will be described in another place.

It is almost impossible to find a region where the cells of the hypodermis are not modified by the presence of the dermal rods. In order to get at the natural appearance of the cells, it is necessary therefore to study them in young specimens, and in the region where the rods are fewest; this region I have found to be near the margin, on the dorsal side. Very thin cross sections of young individuals are the most favorable ones for this purpose.

The cells are columnar, the height necessarily varying with the thickness of the hypodermis. The nuclei are large, have an irregular or sinuous outline, and are situated, as a rule, near the bases of the cells (Figs. 1 and 2). This position is not constant, and depends upon the number and influence of the rhabditi that are present. There is no nucleolus proper, the chromatin being scattered through the nucleus in many large granules. The size of the nucleus does not appear to depend upon the size of the cells; for while the cells in different regions vary to a great extent, the nuclei remain of nearly uniform size.

The cells are finely striated; the striations are most prominent at the basal ends of the cells, and cannot be traced to their free ends. Such radial striations have been described by Böhmig ('86, p. 294) in the hypodermis of Graffilla, and more recently by Lippitsch ('90, p. 328) in the epidermal cells of Derostomum. Iijima ('84, p. 369) also alludes to fine striations in the epidermal cells of Planaria polychroa. The cells do not "etwa flach auf die Basalmembran aufsitzen," but are connected with it by fine processes "welche etwa kammförmig ziemlich dicht neben einander stehen." These processes he believes to be directly continuous with the striations of the cells, and to be protoplasmic prolongations of the cells. He traces them through the basement membrane into the muscles below, thus establishing "eine organische Verbindung zwischen dem Epithel und den Körperinnern." His figure (Taf. XX. Fig. 4) is confusing, and in addition was drawn, as he admits, from a specimen in which the basement membrane exhibited pathological conditions. Besides the striations in the cells, there appear creases or folds resulting from the pressure of the rhabditi.

In thick sections through regions where the rhabditi are numerous, the epidermal cells have the appearance of being joined to the basement membrane by foot-like processes. This appearance at first led me to believe in a condition like that described by Iijima, and it was only after studying sections of material in which the rhabditi had been removed (Fig. 3) that I understood their relations to the cells.

The rhabditi do not lie *in* the hypodermal cells, but *between* them. Kennel ('79, p. 126) and Braun ('81, p. 305) are the only observers who have described them as having an *inter*cellular position. It will be seen from the following description of their development in Phagocata, that such a position is the only natural one. The presence of these rods between the cells produces a crowding, and the pressure is so great that it causes the cells to become displaced and much modified in shape. The nuclei may be pushed out to the free ends of the cells, or crowded down to their bases, and the cells themselves may be so reduced as to appear like mere filaments (Fig. 3). Kennel ('79, p. 126) describes the epidermal cells of Rhynchodesmus after the removal of the rhabditi, as "feine Fädchen . . . so lang als die Epidermis dick ist." Regarding their intercellular position, Braun ('81, p. 305) states for Bothrioplana that the rhabditi "nicht allein zwischen den Zellen stehen, sondern auch das Protoplasma der Zellen durchbohren." In Phagocata, as in Rhynchodesmus, the rhabditi are so numerous that the hypodermis appears at first to be entirely composed of them. As Kennel expresses it, "ausser den feinen, fadenförmigen Zellen kaum etwas anderes Platz zwischen ihnen hat." It is in thick sections, where the epidermis is many layers deep, that the bases of these compressed cells present an appearance as if the hypodermis were connected with the basement membrane by fine foot-like processes. This appearance is only seen where the rhabditi are most numerous. At the lateral edges of the body, where there are few, and where consequently the cells retain their primitive cylindrical form (Fig. 2), the latter are applied to the membrane by their broad bases. It is in these regions also that the striations previously spoken of are most distinctly seen.

Moseley ('74, p. 118) says, "The epidermis here [land planarians] is seen to be made up of large gland-cells and cells containing rod-like bodies and a certain amount of vertical filaments." "The irregular filaments which fill up the interspaces between the gland-cells and rod-like bodies appear to be the remains of the cell-walls and rod-like bodies."

He further says, "The substance of the epidermis is probably made up, in the living condition, of cells resembling the gland-cells described, but of various dimensions, and of cells containing rod-like bodies."

Since the "rod-like bodies," or rhabditi, are really modified glands, Moseley's statement amounts to saying that the epidermis is composed entirely of gland cells, a conclusion which it is not easy to adopt. Moreover, I believe that Moseley's "gland-cells" are only rhabditi that have been modified by the action of the reagent which he used for their demonstration. Kennel ('79, p. 126) obtained similar conditions by the action of chromic and acetic acids on the rhabditi of land planarians. I have found that in Phagocata by the use of picric acid the dermal rods become swollen and granular, resembling the "gland-cells" described and figured by Moseley. "The vertical filaments" were undoubtedly the true epidermal cells, reduced to a filamentous condition by the influence of the many rhabditi lying between them.

I cannot find any organic connection between the cells of the hypodermis and the deeper tissues, such as has been described by Iijima. Although appearances like those described by him do occur, they are secondary conditions, dependent on the presence of the rhabditi and the development of their mother cells. The basement membrane is everywhere traversed by fine tubular processes of the mother cells of the rhabditi, which lie imbedded in the body parenchyma. This fact, together with striations of the cells of the hypodermis and the ultimate reduction of these cells to filaments, might easily lead to conclusions such as those of Iijima. His sections were thick (10–20 μ) both absolutely and in proportion to the length of his largest specimens (20 mm.), whereas my sections were only 5–10 μ in thickness, although the worm attains the length of 35 mm.; moreover, isolation preparations were studied in connection with these sections.

The hypodermis consists of the hypodermal cells and the rhabditi that lie between them. There are no unicellular glands in it. Lang ('84, p. 49) described in Polyclads a granular "interstitial tissue" containing nuclei and pigment which arises, according to his conjecture, from a coalescence of indifferent epithelial cells. Such conditions I cannot find, nor can I detect any cement ("Kittsubstance"), such as that described by Graff ('82, p. 44) for Rhabdocœles.

The dermal rods or *rhabditi* are defined by Graff ('82, p. 49) as "die stark lichtbrechende glasartige homogenen Stäbchen, welche weder einen Faden noch einen Nadel einschliessen und durch ihre glatte Oberfläche, regelmässige Gestalt und ihren Glanz auffallen."

In Phagocata the rhabditi are found in almost every portion of the hypodermis, there being only one region from which they are altogether absent, viz. around the gonopore, where they are gradually replaced by many subcutaneous glands, which open to the exterior in a broad circular area surrounding that orifice. They are present around the oral opening, even up to the aperture, where they abruptly cease. They are most abundant in the middle line on the back, becoming gradually fewer toward the sides and anterior end, but they are again abundant on the ventral surface. They are found over the eyes, and in the epithelium of the two anterior sense organs, where they are well developed but few in number. Iijima ('84, p. 371) has stated that they are wanting in this region in the case of D. lacteum, but are present in Planocera polychroa and Polycelis tenuis. He has also shown that in the case of D. lacteum they are unusually abundant in the region of the genital orifice, both in the epithelium and in the parenchyma, and supposes that they have a sexual significance as urticating organs, the "Liebesfeile" of Schneider; but their absence in this region in Phagocata precludes the assumption that they have in this species any such function.

The rhabditi are all of one kind, but they vary in size. The variations are not local, different sizes occurring wherever rhabditi are found. Some are as long as the hypodermis cells, while others are comparatively short; they vary from 1.5 μ to 16 μ in length. There is an interesting correlation between the thickness of the hypodermal layer and the size of the largest rhabditi; those of the thin hypodermis of the ventral surface are invariably smaller than those of the dorsal side. Each is spindle-shaped, and the outer end is slightly more pointed than the deep end. They stain intensely in the carmine dyes, and then appear perfectly homogeneous; but when stained in Orth's picrocarminate of lithium with an excess of the picric acid, they take on a bright yellow color, and appear more or less swollen and distorted, according to the length of time the dye is allowed to act. Often they have the appearance of hollow capsules filled with granules, or containing a few irregular refractive lumps (Fig. 9). It was probably the swollen and altered rhabditi that Moseley mistook for gland cells. The peripheral portion of the substance of the rhabditi is not affected by the reagent as the contents are. This outward unaltered portion presents the appearance of a capsule, or thick membrane, with a double contour. Moseley says of his glandcells, "The cell appears to have a double wall, for an irregular crumpled membrane is seen often within it."

The rhabditi which lie between the hypodermal cells are not parallel, but are somewhat inclined toward each other, the outer ends generally converging about centres so as to form groups or packets. The small ones lie out near the free surface of the hypodermis; and the largest may reach the basement membrane (Fig. 1). Usually the long axes of the rhabditi are approximately perpendicular to the surface of the epidermis, but they may assume almost any angle with each other; small rods are sometimes seen lying at right angles to neighboring ones.

It was first shown by Oscar Schmidt ('48, p. 6), in 1848, that in the case of Rhabdocœles the rhabditi are developed in subcutaneous flask-shaped cells. Since that time similar conditions have been discovered in all the Triclads. Up to the present time, the development of these cells, "Stäbchenbildungszellen," has not been traced. My studies seem to throw some light on their genesis, and also to show how the rods find their way out between the cells of the epidermis. I first recognized the parent cells in isolation preparations, and saw them in sections only after depigmenting and staining the sections on the slide. Later, I obtained a fresh supply of material, and was able to demonstrate them in abundance, and in all stages of development. They are more easily to be seen on the ventral side of the animal, where they are less obscured by pigment. In their fully developed condition they lie in the body parenchyma immediately beneath the longitudinal muscles. On the ventral side, where the muscle layer is very thick, they may be found in between the strands of the muscles as well as below them. The parent cells have the form of flasks with greatly elongated narrow necks tapering off into long tubular processes, which are traceable outward through the muscles to the basement membrane, and, traversing this, are seen to open out between the cells of the hypodermis. Thus the deep-lying parent cells are in direct communication with the outer world (Figs. 1, 6, and 10). It is by means of these tubular processes that the rhabditi find their way to the exterior, and at length come to occupy positions between the hypodermal cells. I have previously pointed out that the rhabditi in the epidermis lie in groups or packets; presumably each of these groups was at one time contained in a single parent cell.

The connection of the parent cells with the epidermis is a primitive one, for they are only modified cells of the hypodermis, which never cease to retain their connection with that layer. In the earliest stages of development that I have found, they appear like small sacs imbedded in the superficial portion of the longitudinal muscle band, close to the basement membrane, with which they are connected by short necks or tubes (Fig. 4). The cell at this stage contains a single very large nucleus, in which there is no nucleolus, since the chromatin exists, as in the other cells of the hypodermis, in the form of fine particles scattered uniformly through the nucleus. Later, the cell begins to sink deeper into the tissue below the hypodermis, and the tubular neck increases correspondingly in length. The cell contents become finely granular, and appear to grow at the expense of the nucleus, which no longer fills so completely the sac, but becomes smaller and occupies the bottom of the cell (Fig. 7). In the protoplasm surrounding the nucleus, there appear small, round, highly refractive particles that stain deeply. These increase in number and in size, and soon become elongated, taking on the spindle shape so characteristic of the rhabditi (Fig. 6, *rhb.*). During these stages of formation the cell comes to lie in the body parenchyma below the muscle bands, but still retains a connection with the hypodermis by means of its long tubular process. The cells are at length filled with rods, and the nucleus is crowded to the bottom of the cell (Figs. 1, 5, and 10).

The fully developed rods are guided to the exterior by means of the tubular prolongations of the parent cell, and finally make their way through the basement membrane and come to lie between the cells of the hypodermis. The rhabditi, so long as they are contained in the parent cell, are not hard and rigid, but possess a certain amount of plasticity, as can be seen by the manner in which they are bent when many are packed in one cell. This plastic condition of the rods facilitates their passage through the basement membrane. I have been able to find a number of cases such as that represented in Figure 8, where I have shown one of the rods in the act of passing through the membrane. The rods possess this pliability until they leave the deeper tissues, and they attain their definite shape only after they reach the hypodermis, where they become hard and inflexible. After the discharge of the rhabditi, the parent cells become absorbed and disappear.

Anton Schneider ('73, p. 87) says concerning the parent cells, "Sie haben mehrere nach der Haut gehende Ausläufer, deren Epithelzellen reichlich damit gefüllt sind." According to Moseley ('74, p. 119), "The parent cells of the rod-like bodies are arranged beneath the external longitudinal muscular layer at a tolerably even depth; they are, in spirit specimens, of an elongated oval form, with the upper extremity drawn out in a point or long filament, which in some cases may be seen to reach up to the basement membrane." In another place ('74, p. 120) he says, "On treatment with potash, the cells of Bipalium swell up, are seen to contain rod-like bodies, and the fine filament at the upper extremity appears like a duct leading to the surface of the basement membrane."

Hallez and Iijima do not make mention of any processes of the sub-hypodermal parent cells, but believe that the cells are ruptured, and that the rhabditi make their way to the epidermis through the tissues of the body. Hallez ('79, p. 6) says: "Jai été temoin une seule fois de la rupture d'une cellule productrice chez Mesostomum tetragonum; il m'a été impossible de retrouver dans cette cellule rompue la moindre trace du noyau." Iijima ('84, p. 371) writes as follows: "Die Bildungszellen sind rundlich und mit einem ausserordentlich feinkörnigen Inhalt versehen." And again: "Haben die Rhabditen ihre definitive Grösse erreicht, so durchbrechen sie die Zellenwand, welche schlieslich absorbirt zu werden scheint und wandern durch den Bindgewebe und die Basalmembran entweder einzeln oder in Gruppen nach aussen in die Epidermiszellen, in denen sie definitiv verbleiben."

Not all of the rhabditi that are developed in the parent cells of the sub-hypodermal tissue find their way to the exterior. Many of the cells apparently lose their connection with the hypodermis, and their rhabditi are discharged into the body parenchyma; only on this assumption can one explain the presence of the numerous rhabditi that are found scattered in the sub-hypodermal tissues. This condition is not the normal, or at least not the original one. These often occur in large numbers in the zone immediately inside of the longitudinal muscle bands, which is occupied by the mother cells, where they lie in no definite positions, and with their axes directed at all angles.

Rhabditi of all sizes may be developed in the same parent cell. Those of different sizes are not confined to special cells, as found by Schneider ('73, p. 83) and Graff ('74, p. 128) for Mesostomum. Besides the fully developed rhabditi there are in the cells particles that have no constant form, but have the same optical appearance and stain the same as the rhabditi (Figs. 6, 10). These bodies may be either residual matter, disintegrating rhabditi, or incipient rods. They never occur in the epidermis, but are left behind after the discharge of the rhabditi, and by the absorption of the wall of the parent cell they find their way into the body parenchyma, where, with the rods previously referred to, they lie scattered about. Lang ('84, p. 52) found similar bodies along with the rhabditi in Polyclads, and speaks of them as "junge kugelige Stäbchen." I am inclined to regard them as residual secretions.

To my mind it is unquestionable that the parent cells of the rhabditi are of ectodermic origin, as first suggested by Hallez ('79, p. 7). It is only in Triclads and in Rhabdocœls that the mother cells lie in the deeper tissues, and we know so little about the embryology of these groups that we cannot tell just how the passage from the exterior takes place. I have endeavored to show that the cells have a connection with the hypodermis in the earliest stages of their development, long before they show any traces of rhabditi, but whether the cells pass from the hypodermis through the basement membrane, or are separated from the hypodermis before the formation of such a structure, I cannot say. The epidermis of embryos of Mesostomum was found by Graff ('82, p. 56) to be filled with rhabditi, while he could find no traces of the sub-hypodermal parent cells so prominent and abundant in the adult. In Polyclads, the development of the rhabditi is in my opinion identical with that in Triclads; but in the former the parent cells lie permanently in the hypodermis, whereas in the latter they sink down below that layer, where greater opportunity for growth is afforded. The condition found in Polyclads, therefore, I believe to be the primitive one.

Another mode of origin of the parent cells of the rhabditi has been proposed by Loman ('87, p. 69), who considers them to be modified connective-tissue cells that migrate from their original positions in the mesenchyma and pass bodily through the basement membrane, and come to lie eventually between the cells of the hypodermis; or, in the words of the author, "Nach meiner Meinung sind die Stäbchenzellen mesenchymatöse Gebilde, die eine factische Wanderung durch dass sie umgebende Bindgewebe unternehmen, während ihr Inhalt sich zu den fadenförmigen Stäbchen ausbildet. Endlich treten sie durch die Basalmembran (wovon später die Rede sein wird), drängen sich zwischen die Zellen der Oberhaut," etc. Thus according to Loman the parent cells form a part of the hypodermis, and only differ from the conditions found in Polyclads in that their epidermal position is a secondary one. Loman presents no evidence, and in the face of the facts here presented his position is untenable.

Rhabditi are being constantly discharged from the epidermis during the life of the individual, and provision must be made for their renewal. Parent cells are therefore being continually produced to supply the steady demand of the epidermis for rhabditi. The evidence of this lies in the fact that in individuals of all ages these cells are found in all stages of development. Iijima ('84, p. 373) says "es sicher scheint, dass die Rhabditen nicht ausgestossen werden." If the rods are not discharged from the hypodermis, why are they being continually developed throughout the lifetime of the individual? Something must become of them, or there would be an accumulation too great to find room in the hypodermis.

Kennel ('88, p. 474) says, relative to this subject: "Lässt man sie [planarians] aber in Uhrschälchen mit Wasser längere Zeit unbehelligt, so dass sie sich festsetzen, und stört sie dann plötzlich, so ziehen sie sich stark zusammen, machen heftige Bewegungen und suchen zu entfliehen. An der betr. Stelle aber findet man bei schneller Untersuchung Massen von Rhabditen in allen Stadien der Auflösung, und wenn man das Wasser schnell ausgiesst, findet man dort ein Klümpchen zähen Schleim, — die Stäbchen lösen sich in Schleim auf." I have often repeated the experiment of Kennel, and have always found rhabditi in large numbers in the slime secreted by the worm when placed on a glass plate.

We may now consider the question of the morphological and physiological meaning of the rhabditi. Two interpretations of the morphological value of the dermal rods have been given by naturalists. The larger number of observers consider them homologous with the nematocysts[1] of Cœlenterates; whereas the more recent investigators believe them to be the morphological equivalents of gland secretions. I coincide with the latter explanation, and offer the following arguments in its support. The parent cells are unicellular glands, and the rhabditi, their secretions, like the secretions of other dermal glands, are voided from the body of the individual. The rods cannot function as organs of touch in lending resistance to the epidermis, as suggested by Max Schultze and maintained by many others, for they do not lie in the epidermis cells, but between them. The insensible gradations that exist between rhabditi and the secretions of glands, as exemplified in the so called "Pseudorhabditen," "Schleimstäbchen," "Schleimblöckchen," and "Körnerdrüsen," have been to me one of the most striking evidences of the glandular significance of the rhabditi. The dermal rods of Phagocata, when acted on by reagents, present conditions resembling all the varieties of dermal bodies figured by Lang, and, as I have said elsewhere, I believe that the epidermal "gland-cells" of Moseley were only rhabditi modified by acids. Sub-hypodermal glands and the mother cells of the rods never occur together. Where rhabditi are absent, their place is taken by glands, and *vice versa*. This is illustrated in the region of the gonopore and at the edges of the body. Another proof consists in the fact that the reaction with stains is always the same for both glands and rhabditi. With picrocarmine the effect is most striking. All the tissues of the body take the carmine except the rhabditi and the glands, both of which, owing to their yellow color, stand out in contrast to the rest of the body.

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[1] According to Camillo Schneider ('90, p 375) even the nematocysts are to be considered only as highly specialized secretory-cells derived from simple gland cells.

Keferstein ('68, p. 15) was the first to speak of the rhabditi as glandular secretions, and he called the parent cells "Stäbchendrüsen," and the rods "geformte Schleimmassen." More recently this view has been confirmed by Lang ('84, p. 52) and Kennel ('88, p. 474). The secretions both of the slime glands and of the accessory sexual glands often appear as rod-shaped bodies, and it was evidently this appearance of the secretions occurring around the sexual organs that led Jensen ('78, p. 11) to consider them rhabditi, and to speak of them as urticating organs functional during copulation, — the theory first suggested by Anton Schneider. Similar rod-shaped secretions are figured by Graff, who calls them "Schleimpröpfchen."

If we are to consider the parent cells as glands, what part do the rhabditi play in the economy of the worm? I must agree with Kennel, that the rhabditi are of use to the worm in securing food, and, I may add, serve also for protection. Phagocata, like all planarians, is carnivorous, and observation of its feeding habits has shown me that rhabditi are cast out of the body in large numbers, and that this condensed secretion helps to entangle and disable the prey. If one of the worms be placed on a glass plate with a very little water, it soon becomes hopelessly entangled in its own secretions, and when in this condition placed in abundant water, some minutes elapse before it can free itself and regain its activity. If some of the slime be examined with high powers of the microscope, it will be seen to contain many rhabditi, in all stages of dissolution. The rhabditi dissolve slowly in water, and it is by reason of this slow disintegration that the slime retains a thickness and tenacity that impedes the movements of an organism in contact with it long enough for the worm to lay hold of it with its many pharynges.

The conditions found in parasitic Turbellarians may be mentioned as evidence that this is the function of the rhabditi. Only four parasitic species have been studied histologically, three of which belong to the Rhabdocœles and one to the Triclads. In all of these forms rhabditi are absent, but in their stead are found sub-hypodermal glands which resemble the parent cells of rhabditi, and like them open to the exterior, — another illustration of the complementary occurrence of rhabditi and glands.

Von Ihering ('80, p. 149) states that in the case of Graffilla muricicola, from the kidneys of Murex, concretions and rhabditi are altogether wanting in the epidermis. Their function, he says, is one of protection, and hence they are not needed in a parasite. Lang ('80, p. 108) says of Graffilla tethydicola, from the foot of Tethys, that there are no rhabditi, but "Unmittelbar unter den Haut liegt eine grosse Anzahl eizelliger, birnförmiger, sich hauptsächlich mit Picrocarmine intensiv färbender Drüsen." Graff ('82, p. 375) says, concerning the same species, "Ueberdies finden sich hier unter der Haut zahlreiche einzellige birnförmige Drüsen." Anoplodium parasitica, a parasite in the body cavity of Holothuria tubulosa, also possesses no rhabditi: "Ich habe weder an frischen noch an conservirten Exemplaren von *stäbchenformigen* Körpern oder von irgend einem Pigmente etwas wahrnehmen können." (Graff, '82, p. 376.)

In Planaria limuli, a Triclad ectoparasitic on Limulus polyphemus, I have been unable to find any trace of rhabditi, but have found in abundance sub-hypodermal glands that resemble the parent cells of rhabditi, and like them send long ducts to the epidermis. Graff ('79, p. 203) states regarding this species that there are no true rhabditi; but he speaks of certain "Haftorgane," which he compares to rosettes of rod-like bodies, and then adds: "Die dieselben zusammensetzenden Stäbchen (Haftstäbchen) bilden sich im Innern des Körpers in besonderen Drüsen und färben sich äusserst intensiv in Carmine und Hämatoxylin," — but I could not find these organs.

Thus we see that in parasitic Turbellarians there are no rhabditi, their place being taken by many sub-hypodermal glands. Assuming that the rhabditi are condensed secretions used in securing prey and for protection, the conditions present in parasitic forms are in every way consistent with our conclusions. The only other possible function for the rhabditi is that assumed by Graff ('82, p. 58) and stated by him as follows: "Die plausibelste Anschauung ist auch heute noch die von Schultze gegebene und von Stein auch für die Stäbchen der Infusorien adoptirte, wonach die Stäbchen indem sie dem äussern Drucke einen Widerstand entgegensetzen, in ähnlicher Weise befördernd auf der feinere Tastgefühl der Haut einwirken, wie der Nagel auf Tastvermögen der Fingerspitze." I have shown that on account of their intercellular position the rods probably cannot have such a function; but even if this evidence were considered insufficient to disprove their supposed office, one would have to encounter the objection that so important a function would not be likely to be entirely lost in parasites, particularly in such active ectoparasites as P. limuli, where the parasitism is of such a nature that sensory organs would still be of great importance in the animal's economy.

To summarize, then, *the dermal rods are to be considered as condensed secretions arising in sub-hypodermal unicellular glands of ectodermic origin. All gradations exist between rhabditi and the secretions of normal glands. The rhabditi are being continually cast out of the body, and replaced by new ones developed in new parent cells within the body parenchyma. The connection of the parent cells with the epidermis is a primitive one, and the rods pass to the exterior by means of the tubular ducts formed by the neck of the elongated cells. The rods lie between the cells of the epidermis; they are slowly soluble in water, and are used by the animal in securing food and for protection.*

The *basement membrane* is a homogeneous layer immediately under the hypodermis, the cells of which are directly connected with it. It varies in thickness in different individuals and in different parts of the same individual; 1 μ and 6.5 μ are the extremes that I have found. It stains deeply in all of the carmine dyes, and always takes a darker color than the underlying muscles. A granular condition, such as is mentioned by Iijima ('84, p. 375), does not exist, nor is there any appearance of the fibrous structure described by Lang ('84, p. 63) for Polyclads. Minot ('77, p. 408) states that the basement membrane is composed of circular fibres. The only appearance in Phagocata approaching that described by Minot is seen in surface views of bits of the membrane occurring in isolation preparations, where on one surface there appear parallel markings; but these are no doubt due to the intimate contact of the membrane with the circular muscle fibres. The membrane is closely applied to the muscle fibres, and in longitudinal sections, where the circular muscles are cut across, the inner contour appears uneven, owing to the projecting ridges which it sends into the intermuscular spaces (Figs. 4, 6, 7, and 10); stated in another way, the circular muscles may be said to indent the basement membrane, leaving their impression in the form of parallel grooves on its under surface. In cross sections of the worm, the inner border of the membrane appears perfectly smooth, and parallel to the circular muscles (Fig. 2). The only departure from homogeneity is caused by the fine channels occupied by the processes of the parent cells of the rhabditi (Figs. 1, 4, 6, 7, and 10), and these are only transitory, soon becoming obliterated. Occasionally pigment granules find their way through these openings, and may become caught in the basement membrane.

There can be little doubt that the basement membrane is a product of the hypodermis. There is a direct relation between its thickness and that of the latter; hence it is thickest on the dorsal, and thinnest on the ventral surface of the animal. It is true that the hypodermis is easily separated from the membrane, but on the other hand the intimate relation between the two structures is evident from the manner in which the cells of the former remain attached to the latter after the rhabditi have been removed by partial maceration (Fig. 3); and even when the hypodermis has been entirely removed, the outer contour of the membrane in regions where, in consequence of the presence of many rhabditi, the hypodermal cells have become much compressed, appears irregular, the uneven projections representing the points of attachment of the hypodermal cells. In those regions where the rhabditi are few or absent, the basement membrane presents a comparatively smooth surface. There is no evidence in Phagocata that the membrane is an independent cellular tissue, as in Polyclads, since no traces of structure could be demonstrated, the membrane appearing homogeneous with all of the stains that were employed. In my opinion, therefore, the basement membrane is of hypodermal origin.

The *pigment* in Phagocata occurs in the form of fine granules, of an irregular outline and of a dirty greenish color. It lies principally in the longitudinal bands of muscles between the fibres, so that, when a worm is put under pressure and viewed with moderate powers, the pigment appears as if arranged in parallel rows running lengthwise of the animal. In the deeper tissues, below the muscle bands, the pigment occurs in patches and streaks (Fig. 1). No pigment occurs normally in the hypodermis. There are no special pigment cells; the pigment occurs in the form of distinct separate granules, which are intercellular in position, never intracellular. The origin of pigment as isolated granules might be explained by some such theory as that of Eisig ('87, p. 765), by which it is to be considered as a product of the excretory system, — a kind of utilized excreta.

There are only three systems of *muscles:* the circular, the longitudinal, and the sagittal or dorso-ventral. As compared with the complicated musculature of other fresh-water planarians, that of Phagocata is much simplified, and in this respect it agrees with Gunda sementata (Lang, '81^a, p. 193) and Planaria abscissa (Iijima, '87, p. 344). The circular muscles form a single layer immediately under the basement membrane, to which, as we have seen, they are closely applied. The longitudinal muscles form a thick band inside of the circular layer, and are much thicker on the ventral side (Fig. 10) than on the dorsal (Fig. 1). In cross sections the longitudinal muscles appear separated into bundles, between which the ends of the dorso-ventral fibres are seen passing to the basement membrane, into which they are inserted. I have not been able to find a nucleus in or on either the circular or longitudinal muscle fibres. The nucleus of the dorso-ventral fibres is eccentric, as in the muscles of Planaria torva, figured by Ratzel ('69, p. 275, Taf. XXIII. Fig. 26). In cross sections both circular and longitudinal fibres have an irregular outline and show a differentiation into an outer highly refractive contractile portion and an inner feebly refractive axis (Plate I.). Branching ends were observed only in the sagittal fibres.

A reticulate *mesenchyma* constitutes the greater portion of the substance of the body, occupying all the spaces between the organs. The spaces left by the irregular network formed by the branching cells (Plate II. Fig. 18) are connected with one another, and are to be considered as a kind of pseudocœle; they are filled with a granular perivisceral fluid. The sagittal muscle fibres in some places appear to be directly continuous with branches of the mesenchyma cells (Plate II. Fig. 18, *mu. sag.*), so that by contraction of the muscles the sizes of the spaces would be altered, and thereby the perivisceral fluid would be set in motion, thus establishing an irregular circulation in the pseudocœle. Lang ('84, p. 83) maintains that in the case of Polyclads these spaces are intracellular in their origin, and that the so called perivisceral fluid is the result of a liquefaction of the plasma of the connective-tissue cells, which thus become vesicular, and finally, by the breaking through of their thin walls, form a network. But if the pseudocœlar spaces were intracellular in their origin, as claimed by Lang, it would be more difficult to understand the intimate relation between the muscles and the processes of the reticulated parenchyma cells; it would not, however, be in any way an exceptional condition for muscle fibres to be attached to the prolongations of *stellate* connective-tissue cells, more especially when we consider that the muscle fibres and mesenchyma cells have a common origin. As is well known, the Hertwigs have produced evidence to show that the mesenchymatous muscles of the Pseudocœlous animals are "besonders differenzirte Zellen der Bindesubstanz" ('81, p. 98). Moreover, the mode of origin maintained by Lang is not founded, as far as I understand it, on evidences from embryonic conditions. Graff ('82, p. 72) was unable, from the evidence found in Rhabdocœles, to establish "a distinction between muscle fibres and connective-tissue fibres"; and Hamann ('85, p. 96) has shown that in Echinoderms the connective-tissue cells are in direct continuation with the muscle fibres of mesenchymatous origin. From the study that I have made of the conditions in Phagocata I am convinced that they are like those found in Rhabdocœles.

Imbedded in the mesenchyma are the parent cells of the rhabditi and also the glands that open at the surface in different regions. There are two large accumulations of glands that open to the exterior, one around the gonopore, the other on the ventral surface of the head region. A smaller accumulation exists near the posterior end of the body. The glands that occur in the head region afford important evidence of the morphological equivalence of rhabditi-producing cells and ordinary dermal glands. The deep ends of these glands are located behind the brain, between it and the ovaries, and in passing over the brain they run downward and forward till they open out on the ventral surface of the head close to its anterior margin. They are numerous, and occur in two bundles or groups, one on either side of the median plane of the body. They appear as long sinuous tubes with enlargements or swellings occurring at intervals (Plate II. Fig. 17), but without any evidence of branching, and it has not been possible to distinguish between the gland proper and its duct. Not being uniformly distributed, the finely granular contents of the tubes cause the irregular enlargements referred to. Nuclei could not be detected in any portions of the ducts. The two bundles of glands begin immediately in front of the ovaries, and as they pass forward converge, so that when they pass over the commissure of the brain they are in contact with each other; but they soon diverge again, and make their way to the surface as already described. These two bundles of glands I believe to be the homologues of the "Stäbchenstrassen" found in Rhabdocœles, and most prominently in the Mesostomidæ. Both the position and the course of the glands in Phagocata are identical with those of the "Stäbchenstrassen" in Rhabdocœles, and the "wiederholte Anschwellungen" (A. Schneider, '73, p. 83) in the latter correspond to the repeated enlargements in the former. The glandular organs of Rhabdocœles differ from them only in the nature of their contents. Furthermore, the almost complete absence of rhabditi in the head region of Phagocata strengthens this conclusion. One has only to compare Leuckart's ('52, p. 23) description of Mesostomum and the figures given in Graff's great monograph with the conditions present in Phagocata, at once to recognize the probable equivalence of these structures. A similar but smaller accumulation of glands is found at the posterior extremity of the body in Phagocata, and it is worthy of note that there is likewise in Rhabdocœles an accumulation of rhabditi-secreting organs in the same region. The slime-secreting glands at the extremities of the body are used in Phagocata as a means of attachment, for it is principally by its extremities that the worm fastens itself to objects, as can be seen when one attempts to remove it from the side of the aquarium.

The other glands that are imbedded in the mesenchyma are those which open around the genital orifice. Together with their ducts they resemble in form the parent cells of the rhabditi; they also react like the glands of the head region with all stains. A portion of one of these glands from an isolation preparation is represented in Plate IV. Figure 41.

The *digestive apparatus* of Phagocata is like that of other Triclads, except in regard to the number and arrangement of the pharynges, which form such a striking feature of this species. The form, position, relations, etc. of these pharynges have already (p. 4) been described, and it has also been stated that at the junction of the three main tracts of the intestine there is one pharynx which is larger and more prominent than the rest (Plate II. Fig. 20, *phy. m.*), and that this is the homologue of the single pharynx of other Triclads. There is no difference in histological structure between this median pharynx and those which connect with the lateral tracts. In a cross section of a pharynx (Plate II. Fig. 12) the following layers can be distinguished, beginning from the outside: (1) the fine cilia covering the external surface, (2) the external epithelium, (3) a single layer of longitudinal muscle fibres, (4) a single layer of circular muscles, (5) a wide zone occupied by connective-tissue cells and salivary ducts and traversed by radial muscle fibres, (6) a single layer of longitudinal muscle fibres, (7) a broad band of circular muscle fibres, (8) the internal epithelium, and (9) the cilia lining the lumen (compare also the longitudinal section shown in Fig. 16). The external covering of cilia disappears at a region about two thirds of the distance from the free end of the pharynx toward its insertion on the intestine, and the epithelium there loses its smooth appearance, becoming wrinkled and creased. The cilia that line the lumen of the pharynx are more restricted in their distribution, and are lost at about one third of the way from the extremity, where the internal epithelium also becomes longitudinally folded, many of the folds projecting far into the lumen of the pharynx (Plate II. Fig. 12, *ĕth. i.*). In this portion of the epithelium there are many nuclei, whereas in the ciliated region nuclei cannot be seen. Compare Figures 12 and 16, Figure 12 being a cross section which passes through the non-ciliated portion of the internal epithelium. There are no nuclei anywhere in the external epithelium of the fully developed pharynx, except near its proximal end. By the use of silver nitrate, however, I have been able to demonstrate that the layer is a true epithelium. Isolated pharynges were killed with hot 1% silver nitrate. By using the solution hot, the pharynges were killed in an extended condition. A tangential section through material treated in this way is represented on Plate IV. Fig. 47. I have been unable by any method of staining to demonstrate the presence of nuclei in these cells, the boundaries of which are so plainly brought out by impregnation with silver.

In young pharynges (Plate II. Fig. 14), where the tissues are not fully differentiated, nuclei are to be seen in both the external and internal epithelial coverings, although no trace of them can be found later on. It is not difficult to find pharynges in different stages of development, since the number increases with the age of the individual. The young pharynx begins as a solid bud of tissue projecting into a cavity hollowed out of the mesenchyma. The cavity is lined with a layer of flattened cells, which is continuous with the cell layer covering the young pharynx (Plate II. Fig. 11). The cavity is at first closed on all sides, but eventually communicates with the common pharyngeal chamber. The lumen of the pharynx is formed by an infolding of its free end, which projects into the cavity. Although I have not been able to trace directly all the steps in the invagination, I have seen specimens where the lumen was lined throughout with an epithelium, and where there was as yet no connection with the intestine. The epithelium lining the lumen is continuous with that covering the outer surface of the young pharynx, and hence with that lining the pharyngeal cavity, and it presents the same histological conditions as the latter (Plate II. Fig. 11). Figure 14 represents a cross section of a young pharynx somewhat advanced in development, where the cellular structure of both the inner and outer epithelium is still evident; there are as yet no cilia, and no traces of the longitudinal muscles. I expect to describe in another paper the changes by which the mass of indifferent cells composing the young pharynx is converted into the ultimate histological structures of the mature pharynx.

The outer layer of the pharynx has never been described as possessing a distinctly cellular structure. Moseley ('74, p. 131), in speaking of land planarians, describes "an epithelium in which no definite cell structures could be observed; but it appeared transparent, and marked by vertical lines which might represent separation into cellular elements." Iijima ('84, p. 389) also saw "eine senkrechte Streifung." Lang ('81, p. 196, and '84, p. 109) speaks of it as a "cuticulaänliches Epithel" with flattened nuclei which it was difficult to see, and Minot ('77, p. 426) gives to it a well defined basement membrane. It is obvious from the description that I have given of the young pharynx that the outer layer, though ultimately much modified in appearance, is nevertheless an epithelial layer.

I could not demonstrate the presence of a cuticula with pore canals such as has been described by Iijima ('84, p. 390); neither could I discover anything answering to the nerve plexus described for other forms, nor could I detect any nerve tissue. From the automatic movements of the isolated pharynges, one would expect to find a complicated system of nerves, and perhaps one or more ganglionic centres.

In the mature pharynges the radial muscle fibres run from the outer to the inner epithelium, to both of which they are attached by their finely branched ends (Figs. 12 and 16). These muscles no doubt act antagonistically to the broad band of circular muscles in dilating the lumen of the pharynx, and by means of these two systems the peristaltic motions displayed by the pharynges are accomplished. Between the radial fibres there is a network of connective-tissue cells, and in the outer half of this middle zone occur the salivary ducts (Figs. 12 and 16, *dt. sal.*), which run the whole length of the pharynx and open at the edge of its lip. In the meshes of the connective-tissue network are seen fine granulations; these spaces are undoubtedly in communication with the pseudocœle of the body mesenchyma, and it is to the coagulation of the perivisceral fluid which has made its way out into the tissues of the pharynges that is due the granular appearance seen.

I have little to add to what has been written concerning the histology of the intestine, my observations agreeing in the main with those of Iijima. The structure is the same in the principal tracts and in the smaller branches; there are no differentiated gland cells. During the periods of most active digestion the intestinal cells are filled with highly refractive oil-like globules, of different sizes (Plate IV. Fig. 43), — the food matter absorbed by the cells. In this condition the cells are large, and protrude into the lumen, so that in the smaller branches of the intestine the latter has entirely disappeared. The contents of the cells are eventually absorbed by the neighboring tissues, and the intestinal cells themselves then appear vacuolated.

I have not been able to trace out the course of the *excretory canals.* Although I have endeavored many times to study them, I have never seen more than a few loops in the head region, and these were seen only when the animal was put under great pressure, resulting in disintegration of the tissues.

The *nervous system* of Phagocata agrees in the main with the descriptions given by Lang ('81, p. 53) and Iijima ('87, p. 349) for other planarians. The longitudinal nerve trunks unite near the anterior end of the body in a well developed brain mass (Plate III. Figs. 25 and 33), and posteriorly are connected with one another by fine commissures. Larger commissures unite the trunks to one another throughout their whole length, either running straight from trunk to trunk, or branching in their passage (Plate IV. Fig. 38). The latter condition may be regarded as closely related to one in which two commissures are united to each other by means of a connective, a condition that often occurs. There is no fixed relation between the number of transverse commissures and the lateral diverticulæ of the intestine, but lateral nerves are usually given off from the main stems at points opposite to the union of the latter with transverse commissures (Plate IV. Fig. 38). The main nerve trunks are prolonged anterior to the brain. They diminish rapidly in size, and give off several lateral branches, which are directed obliquely forwards and outwards (Plate III. Figs. 25 and 36), and they finally break up into minute branches which form a network. The lateral nerves from the main trunks run, sometimes with, sometimes without branching, to the margins, where they unite with a second pair of finer longitudinal nerves, — the marginal or peripheral nerves (Plate IV. Fig. 37, *n. pi'ph.*). The marginal nerves form the lateral edges of a great nervous network, which lies near the ventral surface just inside the sheet of longitudinal muscles. Figures 37 and 38 represent portions of two successive horizontal sections close to the ventral surface. The sections are 30 μ thick, and pass through the floor of the pharyngeal chamber; the light areas show where the knife has cut through the wall into the pharyngeal cavity. The animal having been sectioned from the ventral side, Figure 38 is the deeper (i. e. more dorsal) section. The position of the oral opening (*o*) indicates that the portions of the sections shown are from the same region of the body. In Figure 38 are seen the main nerve trunks (*n. l.'p.*) together with transverse commissures (*com. t.*) and lateral nerves (*n. l.*). It may be seen from Figure 37 how the median branches from the peripheral nerves (*n. pi'ph.*) break up into a network or plexus, which is distributed to the muscles (*plx. mu.*). This network covers the whole of the ventral surface, and at the extreme anterior end of the body is continuous with finer ramifications of the anterior longitudinal trunks. I could find no trace of a similar plexus in connection with the less developed muscles of the dorsal side.

The nervous system of planarians may be readily understood, it seems to me, if we regard it as composed of two more or less distinct parts, — a deep-seated and a more superficial portion. The deep-seated and more central part is present in all planarians hitherto investigated, and consists of the brain, longitudinal nerve trunks, their commissures, and the lateral nerves given off from them. The superficial portion consists of a nerve plexus which lies just underneath the longitudinal muscles, and may be confined to one or the other of the two surfaces, or may be wholly wanting. A conspicuous part of this superficial system, whenever it exists, is the marginal nerve. The connection between the deep and superficial portions of the nervous system is effected by means of vertical nerves running between the two, and, as I have found in Phagocata, the marginal nerve also serves in an indirect way the same purpose; for on the one hand it is connected with the lateral nerves of the central system, and on the other it forms the marginal terminus of the superficial system.

Lang ('81, p. 72) has described in Gunda a marginal nerve directly connected with the lateral nerves given off from the main trunks, but has been unable to find any other evidence of a plexus. In Rhynchodesmus, according to the same author ('81, p. 62), there are both dorsal and ventral plexuses, which are in contact with the deep surfaces of the longitudinal muscles, and are connected with the central system by vertical branches from the main trunks, from the lateral nerves, and from the transverse commissures, but there is no peripheral nerve. Lang ('81, p. 57) also finds a plexus in connection with the deeper longitudinal muscles in Planaria torva. Iijima ('84, p. 426) has likewise found a dorsal plexus in a similar position in Pl. polychroa and in D. lacteum, and Loman ('87, p. 76) has found the same conditions in Bipalium sumatrense and B. javanum. In Gunda ulvæ and Pl. abscissa there exists, according to Iijima ('87, p. 349), a second, dorsal pair of longitudinal stems, giving off branches that break up into a plexus and unite with the plexus from the lateral branches of the main trunks, the whole forming a "Nervenschlauch." He says that a "Randnerv" is present, but he does not state what are its relations to the plexuses.

From this brief survey it is obvious that Gunda represents one extreme, and Rhynchodesmus the other; since in the former there are no superficial plexuses, and in the latter there is a superficial plexus on both dorsal and ventral surfaces in addition to the parts found in Gunda, except that Rhynchodesmus has no marginal nerve. Both Phagocata and Planaria abscissa are intermediate between these extremes, Pl. abscissa possessing only the dorsal portion of the superficial system (in which a special dorsal longitudinal nerve has arisen), and Phagocata having only the ventral portion of that system. Both possess, however, the marginal nerve found in Gunda, and I believe that it probably sustains in Pl. abscissa the same relations to the deep portion of the nervous system that I have found to exist in Phagocata.

It is evident, I think, from what I have shown in Phagocata, that the marginal nerve is to be regarded as one of the means of communication between the central and superficial parts of the nervous system; or perhaps rather as a differentiation of that portion of the superficial system which is put in connection with the deep system by means of the lateral branches from the main trunks.

It may perhaps be reasonable to suppose that the more concentrated condition in Gunda has been brought about by a process of centralization from the more diffuse and more primitive (?) condition shown in Rhynchodesmus.

The brain is formed on the same plan as that of Gunda (Lang, '81, p. 67; '81^a, p. 213). I find two commissures, a larger anterior commissure which Lang calls in Gunda the sensory, and a smaller posterior one which he calls motor (Plate III. Figs. 23, 33, and Plate IV. Figs. 39, 46). The posterior commissure lies somewhat behind and below the anterior one. It directly connects the longitudinal nerve trunks, since it lies in the same ventral plane with them, while the anterior commissure, occupying a higher plane, is only indirectly united to these; viz. by means of the lateral masses of the brain from which vertical commissural fibres (the motor-sensory commissures of Lang) extend to the nerve trunks. Lang describes four pairs of nerves as arising from the lateral sensory masses of the brain. I cannot discover that there is any fixed number in Phagocata. The only well defined one is the optic nerve (Plate IV. Fig. 40, *n. opt.*). A great sheet of fine nerves is given off from the lateral surface of the brain, and, spreading out fan-like, runs forward to the anterior margin of the body (Plate III. Figs. 25 and 34, *n.*). It is from these nerves that the "Tastorgane" of this highly sensitive portion of the body receive their nerve supply.

A comparison of the figures will make clear the relation of the different parts of the brain. Figures 26 to 31 are from cross sections through the region of the brain taken at intervals of 60 μ. Figures 32 to 36 are consecutive sections in the horizontal plane, Figure 32 being the most dorsal of the series.

Lang ('81, p. 79) speaks of a "Zellenbeleg von wirklichen Ganglienzellen" around the brain of Triclads. Iijima ('87, p. 353) describes these cells as being unipolar with extremely delicate processes. I also find a layer of closely packed cells with large nuclei around the brain, more especially about the so called sensory portions (Plate III. Figs. 26–31, Plate IV. Figs. 39 and 40), but I cannot say that these are ganglionic cells. They resemble in every way connective-tissue cells; they react like them with stains, and are more prominent only on account of their compact arrangement. The nuclei of the two large "Substanzinseln" in the lateral masses of the brain (Plate III. Figs. 28, 33, Plate IV. Fig. 39, *con't. tis.*) are both identical and continuous with the nuclei surrounding the brain, and those found in the main nerve trunks cannot be distinguished from them. The ganglionic cells occurring *in* the nerve tissue are not as large, nor do their nuclei stain as deeply, as those occurring *around* the brain mass. I therefore believe that the latter belong to the mesenchyma, and that the "Substanzinseln" are only intrusive connective tissue.[1] Aside from this, I can add nothing to the observations of Iijima on the finer structure of the nervous tissue. The longitudinal nerve trunks in some places appear to be double for a considerable distance, being split, as it were, by the ingrowth of mesenchymatous tissue (Plate III. Figs. 33 to 36, and Plate IV. Fig. 38). All such openings, as pointed out by Lang ('81, p. 56), occur between the points of origin of the lateral nerves.

The *testes* are numerous, and are found lying close together throughout the whole length of the animal. Their development takes place before that of the yolk glands. While the latter are still in an early stage of development, spermatogenesis has been completed, the testes have disappeared, and the spermatozoa are found filling the vasa deferentia. The testes first appear as spherical clusters of cells, which by division increase in number and arrange themselves in the form of hollow spheres. Some of the peripheral cells divide rapidly into small spherical cells, that come to lie in the cavity of the testis. These cells become elongated or pear-shaped, and are then differentiated into two portions, a deeply stainable thickened end, and a tapering tail portion (Plate II. Fig. 24). Further elongation takes place, until the form of the adult spermatozoön is reached. Many stages of development can be seen in the same testis. The different stages occur in distinct groups, each group probably being the product of one of the parent cells. The wall of the testis, when the spermatozoa first begin to develop, is composed of many cells, most of which by division go to form spermatozoa; a few of the cells, however, are differentiated into flattened epithelium, which constitutes the wall of the capsular testis (Plate II. Fig. 24, *e'th.*).

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[1] Since I came to these conclusions in regard to the mesenchymatous character of the so called "Substanzinseln," I have been gratified to learn that my conclusions agree with those of Loman ('87, p. 77). In Bipalium, then, as well as in Phagocata, the "Substanzinseln" present in all particulars the same differences from ganglionic cells.

I have not succeeded in ascertaining the exact manner in which the spermatozoa find their way into the vasa deferentia, but Iijima's statement ('84, p. 408) that they do not wander through the spaces of the mesenchyma is certainly incorrect. The testes give rise to tubular prolongations, but whether these are directly connected with the vas deferens or first unite into one or more vasa efferentia, I cannot say. The testicular canals appear to be direct outgrowths of the wall of the testis. Their walls and those of the vasa deferentia have the same simple structure (compare Plate II. Figs. 23 and 24), being composed of a single layer of thin epithelium. The nuclei in the walls of the tubes often occur in pairs, and thus suggest that the cells to which they belong have recently undergone division (Fig. 24).

According to Moseley ('74, p. 139), the testes in land planarians open directly into the vasa deferentia; Minot ('77, p. 432), on the contrary, speaks of fine testicular canals that unite to form larger tubes. Kennel ('79, p. 137) states that the testes, arranged in rows, fuse to form the vasa deferentia.

The anterior ends of the vasa deferentia in Phagocata lie on either side of the pharyngeal chamber in the region of the mouth opening. They have the form of large elongated sacs (Plate IV. Fig. 42, *x*) which open into comparatively narrow tubes (*va. df.*), which are of an even calibre, and much convoluted and twisted. They run backward parallel to each other until near the base of the penis; they then turn at right angles toward the middle plane, where they unite to form a single tube which terminates at the apex of the penis. The spermatozoa when ripe leave the testes by the testicular canals previously described, and pass into the vasa deferentia, which become filled from their enlarged blind ends up to a point beyond that where they unite to enter the penis. Here the spermatozoa remain stored until arranged into spermatophores, in which form they pass into the vagina of another individual. After the spermatozoa have found their way to the vasa deferentia, all traces of the testes disappear.

Physiologically considered, the vasa deferentia of Triclads are to be considered as vesiculæ seminales. In Polyclads and in Rhabdocœles a vesicula seminalis is present. This organ has been described for land planarians by Moseley ('77, p. 278) and Loman ('87, p. 81), and Kennel ('88, p. 460) speaks of "mehrfach gewundenen Samenblasen" in Planaria alpina. There can be no doubt that the terminal enlargements found in Phagocata are a provision for the storage of a great number of spermatozoa, as their size is found to vary in different individuals and on different sides of the same individual according as the number of spermatozoa is large or small.

The *penis* or intromittent organ is a highly muscular plug-like structure (Plate IV. Fig. 42, *pe.*) that lies in the genital atrium or penis sheath. It is covered with a flattened epithelium, under which there are alternating layers of circular and longitudinal muscles, five of each, forming a thick zone. Immediately outside the epithelial lining of the tube there is a band of circular muscles, and between these and the outer muscles there is a broad zone occupied by a meshwork of muscular fibres, prominent among which are those having a radial direction. The lumen of the penis is not of an even calibre, but consists of a succession of chambers, or dilatations, lined with a granular epithelium, which is probably glandular. It is within the lumen of the penis, no doubt, that the spermatophores are formed. The sheath of the penis is lined with an epithelium of cylindrical cells, the nuclei of which lie close to the bases of the cells, and are stained deeply, while the glandular cell substance is stained only slightly. These cells also may be glandular, but if so, I can find no explanation for their faint reaction with staining reagents. In that respect they differ from all other glandular tissue.

The female sexual organs consist of a pair of ovaries with their oviducts, the vitellarium or yolk gland, the uterus, and the vagina. The single pair of *ovaries* is situated in the anterior part of the body a little behind the brain mass. They are symmetrically placed on the ventral side of the body just dorsad of the main nerve trunks, one on either side. They appear as rounded sacs filled with ova (Plate II. Fig. 21). The wall of the ovary is a delicate membrane, in which I could detect no sign of cell structure, such as Moseley ('74, p. 137) found in the ovary of land planarians. Scattered in between the ova are the nuclei of a connective-tissue network that fills the spaces between the ova (Plate II. Fig. 21, *nl. con't. tis.*). Iijima ('84, p. 412) considers the branching cells between the ova as rudimentary egg cells, at whose expense the ova develop. I have not yet seen different stages in the development of the ova.

Intimately associated with the ovaries are two prominent compact cell masses with deeply stained nuclei, which may provisionally be called *parovaria* (Plate II. Fig. 21, *vt'm.*). They are larger than the ovaries, and envelop them above, in front, and on the outside; that is to say, the ovaries are surrounded on three sides, being partially imbedded, so to speak, in these cell masses. The latter are present in every individual, and their size relative to that of the ovaries varies only with the condition of the sexual organs. They are smallest during the development of the spermatozoa, and are most prominent at the time when the yolk glands have reached their full development. For a long time these cell masses puzzled me. I believed them to correspond to the second pair of rudimentary ovaries described by Iijima ('84, p. 412) for Polycelis tenuis, and I at first accepted his interpretation of their significance; but sections through additional material, where the female organs were not so advanced, served to show their true meaning; *they are the organs which give rise to the yolk glands.* At an early stage in the development of the testes no yolk glands are present, but they begin to appear at the time when the spermatozoa are ripening.

The first traces of the *yolk glands* are seen in branching chains of cells, which arise as outgrowths from the parovaria. Each cell has a large nucleus that is stained deeply in carmine. In these chains the cells lie either in a single row, or it may be in several rows (Plate II. Figs. 19 and 19*a*). The nuclei are large and granular, and occupy the greater part of the cell. It is to be inferred that the cells are dividing rapidly, since nuclei are found in all stages of division, and two nuclei are frequently seen in the same cell; the division appears to be direct, or amitotic (Plate II. Figs. 19 and 22). The rudimentary yolk glands occupy at first the ventral regions around the oviducts, but afterwards they send branches from there dorsad, until there is formed a dendritic system of rapidly dividing cells, which ramify through the tissues. From each of the cell masses around the ovaries is derived one half of the yolk system, that belonging to its own side of the body. The cell chains of the young yolk glands are seen to be directly connected with the parovarial cell masses, and histologically the structure of the two is identical (compare Fig. 19 with Fig. 22, Plate II.). Furthermore, at the time of development of the yolk glands there is a very active division of the cells of the parovarial masses, a condition that does not exist when the yolk glands have matured. A similarity in the condition of the cells of the yolk glands and those of the parovarial masses is evident at all stages of development. The young cells of the yolk glands increase in size, but do not grow as rapidly as the surrounding protoplasm, and therefore the nucleus becomes smaller in proportion to the size of the cells. Many highly refractive granules appear in the protoplasm, and increase in number with the growth of the cells, till eventually, when the cells have attained their full size, they form a relatively large proportion of the cell mass (Plate IV. Fig. 45). Corresponding to the changes that take place in the yolk cells, there is a slight increase in the size of the parovarial cells, in which there is also an accumulation of highly refractive granules (Plate IV. Fig. 44), but the nuclei retain more nearly their original proportions to the cells than in the case of the yolk cells. In addition to the identity of histological structure, a most striking evidence of the derivation of the yolk glands from the parovarial cell masses is found in the reaction of both kinds of cells with staining fluids, more especially with picrocarminate of lithium. Figures 44 and 45, Plate IV., represent respectively sections through parovarial cells and mature yolk-gland cells of the same individual. Figures 19 and 22, Plate II., are sections from another individual; Figure 22 is a section of young parovarial cells, and Figure 19 of incipient yolk-gland cells. Upon comparison of Figures 19 and 22 with Figures 45 and 44, it will be noticed that, in addition to the appearance of the granules in the protoplasm of the older cells, there has been an increase in the size both of the yolk cells and of the cells of the parovarium. It is my belief, then, that the two large dendritic yolk glands arise by cell proliferation from the parovarial organs which exist in intimate relation with the ovaries.

Iijima ('84, p. 412) describes a pair of structures lying in front of the ovaries in Polycelis tenuis as being composed of a solid mass of cells, and as resembling young ovaries, so that this species possesses, in his opinion, two pairs of ovaries, one of which is rudimentary. On account of their terminal position, he considers these rudimentary structures, although not the functional ovaries, as the homologues of the single pair of ovaries present in other species. His account of the growth of the yolk glands, as given at p. 417, coincides with my observations, but concerning the source of the chains of young yolk cells he says (p. 455): "Wir dürfen sagen, dass die Dotterstränge durch Vermehrung einzelner Zellen, welche in dem Mesenchym sich befinden, ihren Ursprung nehmen." But his evidence that the "Dotterstränge" arise *in situ* is not satisfactory. It is to be regretted that he has not given a fuller account of the so called rudimentary ovaries of Polycelis, which, I am almost certain, are the equivalents of the parovarial cell masses of Phagocata.

The absence of yolk glands in Moseley's land planarians can be accounted for by assuming that in his material they were not yet ripe, as was probably the case. He states ('74, p. 137), however, that there is occasionally present in Bipalium, "just externally to the lower extremities of the ovaries, a small mass of large nucleated cells connected by a pedicle with the ovary itself." He considers that "it may represent a yolk-gland in a rudimentary condition." With this I fully agree, and further believe that this rudimentary yolk gland is the homologue of the structure which in Phagocata I have called parovarium.

The presence of a vitellogenous organ in Phagocata, together with the condition found in Polycelis by Iijima and in Bipalium by Moseley, suggests a discussion of the relations of the ovaries and vitellaria. Yolk glands have long been considered as resulting from the differentiation of the ovaries. Gegenbaur, as stated in his text-book ('70, p. 281), considers the yolk glands to be "Theile eines ansehnliches Ovars." Hallez ('79, p. 63) maintains that "le *vitellogène* n'est autre chose qu'une partie différenciée de l'ovaire," and according to Lang ('81ª, p. 228), "Die Keimstöcke und Dotterstöcke der Tricladen sind einander gleichwerthig. Sie entstehen aus Zellen, die anfangs nicht von einander unterscheiden lassen." Among Rhabdocœles all gradations are found, from an undifferentiated "Keimdotterstock," where ova and yolk cells are developed in different portions of the same organ, to conditions in which the ova and yolk cells are produced in distinct and separate organs. The yolk glands, then, have arisen by a divison of labor from a simple germ gland, as has already been formulated by Graff ('82, p. 130) in the following words: "Die Keimdotterstöcke müssen wir uns aus Ovarien durch einfache Arbeitstheilung hervorgegangen denken; durch räumliche Trennung der verschieden functionirenden Abschnitte des Keimdotterstockes entstanden schlieslich die Keim- und Dotterstöcke." I consider the condition found in Phagocata to be less differentiated than that exhibited by Pl. tenuis (Iijima), inasmuch as the cells which form it still retain a more intimate relation to the true ovary than they do in the latter case.

The union of the yolk glands with the oviducts is a secondary one; it takes place at intervals throughout their length. I have not studied this in detail, but, as far as I have learned, the conditions agree with the careful description given by Iijima ('84, p. 415). The oviducts open into the vagina just above the point where it enters the genital atrium (Plate IV. Fig. 42).

The *uterus* (Plate IV. Fig. 42, *ut.*) is a sac-like organ lying just anterior to the penis, and has thick walls that are thrown into many folds. It is lined with an epithelium of elongated cylindrical or pyriform cells of a glandular nature. The appearance of the cells varies with the activity of their secretion; the protoplasm may be either homogeneous, or filled with oil-like globules, or it may be vacuolated. The cells rest upon a fine basement membrane. There is no musculature, and there are no cilia.

The mouth of the uterus is prolonged into a tube with thick muscular walls, *the vagina* (Plate IV. Fig. 42, *vag.*), which runs backward, passing above and to the left of the penis and then dipping down toward the ventral side of the body, where it opens into the genital atrium. Where the vagina arises from the uterus it is lined with a ciliated epithelium of low cubical cells, and possesses a musculature of circular and longitudinal fibres. As it passes backward, the cells of the lining epithelium become taller and cylindrical (Plate II. Fig. 15, *e'th.*), and the nuclei are elongated. The outer ends of the cells show distinct granulations, and the contour of the lumen becomes uneven; the glandular nature of the cells now becomes apparent. Along with the change in the appearance of the cells of the lining epithelium there is an increase in the thickness of the musculature, which now consists of alternating layers of circular and longitudinal fibres. The musculature of the vagina reaches its greatest development at the point where it bends toward the ventral side of the body; from this point onward the cells lose their glandular character, and the musculature diminishes in thickness, till, at the point where the vagina receives the oviducts, it again consists of only a single layer each of circular and longitudinal fibres. Moseley ('74, p. 141) and Iijima ('84, p. 420) speak of radial fibres in the walls of the vagina; but I could not find any.

The accessory female organs of Triclads have been the subject of much discussion. There are no other structures about which so many opinions at variance with each other have been advanced. The organ which I have called the uterus is regarded by Iijima ('84, p. 419) as a simple gland whose secretions go to form the cocoon. In his opinion, it has no function in connection with the union of the sexual elements; he considers it homologous with the shell gland of Cestodes and Trematodes. According to Kennel ('88, p. 458), it is to be considered as a receptaculum seminis, and its secretions serve to preserve the spermatozoa. Hallez ('87, p. 24) maintains that fecundation takes place in the uterus, and that in it the yolk cells join the egg cells. According to Hallez, there is a division of labor among the cells lining the uterus. The majority of them secrete the substance of the cocoon, others secrete "un liquide spécial" to support the vitality of the male elements, and possibly to aid in fecundation. He states that in Pl. polychroa the cocoon is produced in the uterus, but as regards Dendrocœlum lacteum he agrees with Iijima in maintaining that the cocoon is formed in the genital cloaca or atrium. In Phagocata I have found ova as well as spermatozoa in the uterus, and believe that fecundation takes place there. The spermatophores are deposited in the vagina and from there the spermatozoa make their way into the uterus. I believe also that a portion of the contents of the cocoon are secreted by the uterus, but that the substance of its wall, the shell, is produced from the glandular lining of the vagina, so that in Phagocata at least the "uterus" cannot be regarded as homologous with the shell gland of Cestodes. It is my purpose to discuss at length these questions, together with that of the formation of the spermatophore, in a subsequent paper on the embryology of this species.

No organ comparable with the "muskulösen Drüsenorgan" of Iijima ('84, p. 422), or the "vésicule (bourse) copulatrice" of Hallez ('79, p. 57, and '87, p. 20), is present.

Summary.

Phagocata differs from all known Triclads in possessing, besides a pharnyx which opens into the intestine at the junction of its three main trunks, many additional pharyngês which are joined to the two lateral trunks of the intestine. The lateral pharynges are histologically identical with the median one; they differ from the latter only in size; the more remote they are from it, the smaller they are.

The rhabditi or dermal rods lie between the cells of the hypodermis, not in them. They are developed in cells lying in the sub-hypodermal mesenchyma; the cells are connected with the hypodermis by fine tubular prolongations. The connection of the parent cells of the rhabditi with the exterior is a primitive one, and the rods enter the hypodermis by emergence along these prolongations. The rhabditi are ultimately discharged from the hypodermis, and new ones are constantly being developed in new parent cells. They are slowly soluble in water, and are used for securing prey and for protection.

The parent cells of the rhabditi are unicellular glands, and the rods are their condensed secretions.

The "Stäbchenstrassen" of Rhabdocœles are homologous with the slime glands in Phagocata.

The basement membrane is a product of the hypodermis. It is structureless.

The pigment is intercellular, occurring in the form of scattered granules.

The pseudocœlar spaces of the mesenchyma are intercellular in origin, and sagittal muscles are directly continuous with processes of the mesenchyma cells.

The nervous system consists of a deeper and a superficial portion; a marginal nerve indirectly connects the two. The condition in Phagocata may be intermediate between that of Gunda and Rhynchodesmus.

The brain presents two commissures, an anterior and a posterior one, uniting the longitudinal nerve trunks. The so called "Substanzinseln" are intrusive connective tissue.

The testes give rise to tubular outgrowths, the vasa efferentia. The vasa deferentia have terminal enlargements and function as vesiculæ seminales.

The yolk glands arise by cell proliferation from two cell masses, the parovaria, which are in immediate contact with the ovaries. The intimate connection of the parovaria with the ovaries indicates the differentiation of the ovary and vitellarium from a common gland.

The so called uterus is not only a gland; it is a place in which the sexual elements are brought together, and where fertilization consequently takes place.

CAMBRIDGE, August, 1890.

It was not until this paper had gone to press that I had access to the recent work of Böhmig ('91) on Rhabdocœles. It was then too late for any detailed review. I am gratified to observe, however, that he has arrived at conclusions from his studies of Rhabdocœles which agree in many points with those which I have expressed in the foregoing paper, especially in his statements as to the fate and significance of rhabditi.

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EXPLANATION OF FIGURES.

All the figures are from camera drawings of Phagocata gracilis, Leidy.

ABBREVIATIONS.

atr.	Genital atrium.
cil.	Cilia.
cl. rhb.	Parent cells of the rhabditi.
cl. sp'z.	Parent cells of the spermatozoa.
com. a.	Anterior commissure of the brain.
com. p.	Posterior commissure of the brain.
com. t.	Transverse commissure.
con't. tis.	Connective tissue.
dt. sal.	Salivary duct.
e'th.	Epithelium.
e'th. ex.	External epithelium.
e'th. i.	Internal epithelium.
e'th. phy.	Epithelium of pharynx.
go'po.	Gonopore.
h'drm.	Hypodermis.
h'drm.'	Aborted cells of hypodermis.
in.	Intestine.
mb. ba.	Basement membrane.
ms'chy.	Mesenchyma.
mu. crc.	Circular muscles.
mu. crc. ex.	External circular muscles.
mu. crc. i.	Internal circular muscles.
mu. l.	Longitudinal muscles.
mu. l. ex.	External longitudinal muscles.
mu. l. i.	Internal longitudinal muscles.
mu. r.	Radial muscles.
mu. sag.	Sagittal muscles.
n.	Sensory nerve.
n. l.	Lateral nerve.
n. l.'a.	Anterior longitudinal nerve.
nl. con't. tis.	Nucleus of connective tissue.
nl. e'th.	Nucleus of epithelium.
n. l.'p.	Posterior longitudinal nerve.
nl. rhb.	Nucleus of parent cells of the rhabditi.
n. opt.	Optic nerve.
n. pi'ph.	Peripheral (marginal) nerve.
o.	Mouth opening.
oc.	Eye.
ov'dt.	Oviduct.
pe.	Penis.
phy. m.	Median pharynx.
phy. l.	Lateral pharynx.
plx. mu.	Nerves to muscular plexus.
rhb.	Rhabditi.
sec.	Secretions which do not form rhabditi.
sp'z.	Spermatozoa.
trn. i. a.	Anterior trunk of intestine.
trn. i. l.	Lateral trunk of intestine.
ut.	Uterus.
va. df.	Vasa deferentia.
vag.	Vagina.
vt'm.	Parovarium (vitellarium).
x.	Enlarged ends of vasa deferentia.

PLATE I.

Fig. 1. Portion of a longitudinal section of the dorsal wall of the body, showing the parent cells of the rhabditi and the position of the rhabditi in the hypodermis. × 900.

" 2. Cross section near the lateral margin of the dorsal side, in a region where there were no rhabditi, showing the hypodermis in its primitive condition. × 900.

In Figures 1 and 2 the basement membrane did not take the stain.

" 3. Longitudinal section through a region where there were many rhabditi which have been removed by partial maceration, showing the modified condition of the hypodermal cells due to the crowding of the rhabditi. × 900.

" 4. Longitudinal section of ventral wall of body, showing a young parent cell of the rhabditi, the nucleus almost filling the cell. The hypodermis removed. × 900.

" 5. Two parent cells of the rhabditi, from macerated material. × 960.

" 6. Longitudinal section of ventral wall showing two stages in the development of the parent cells of the rhabditi. Two small rhabditi have already been secreted in the larger cell. The hypodermis removed. × 900.

" 7. Stage in the development of the parent cells of the rhabditi next older than that shown in Figure 4. The cell has sunk deeper into the tissues, and the nucleus is smaller in relation to the size of the cell. Ventral wall of body, the hypodermis being removed. × 900.

" 8. Longitudinal section of ventral wall showing one of the rhabditi in the act of passing through the basement membrane. The hypodermis removed. × 900.

" 9. Showing the appearance of the rhabditi after having been acted upon by picric acid. × 900.

" 10. Longitudinal section of the ventral wall showing one of the parent cells of the rhabditi filled with the rods. The remnants of another cell represented by the nucleus and three rhabditi are seen close by. The hypodermis has been removed. × 900.

Owing to a mistake of the lithographer, the nuclei of the parent cell (*nl. rhb.*) in Figure 10 are not represented as being granular, as they should be.

WOODWORTH PHAGOCATA.

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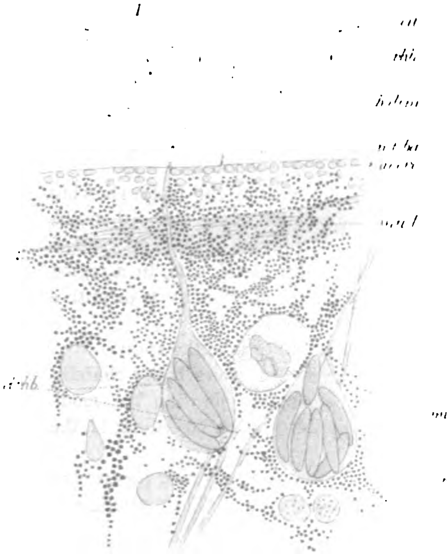

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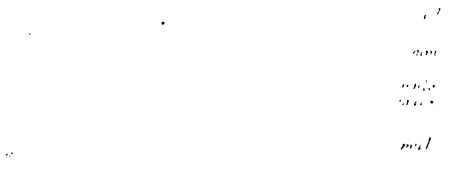

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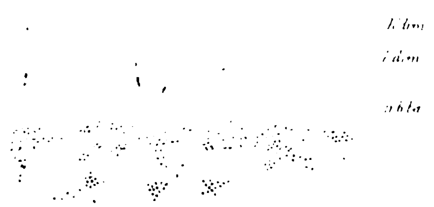

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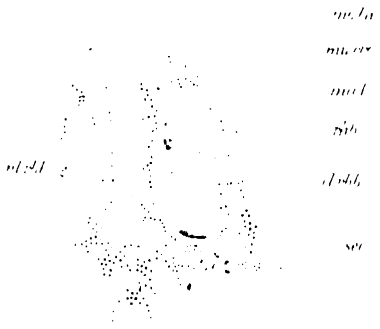

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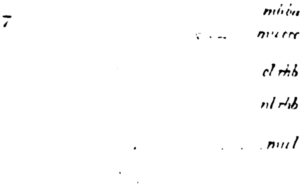

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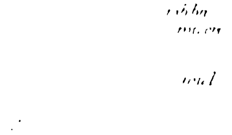

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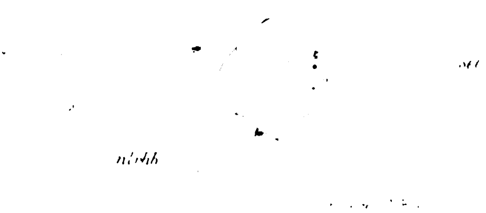


PLATE II.

Fig. 11. Cross section of an individual in the region of a young budding pharynx. Its connection with the intestine has not yet been established. × 300.

" 12. Portion of a cross section through one of the lateral pharynges. × 320.

" 13. A worm feeding on an Annelid; five of the pharynges are visible. Killed with hot corrosive sublimate while feeding. × 10.

" 14. Portion of a cross section through young pharynx, showing the nucleated epithelia. The other tissues are not yet differentiated. × 300.

" 15. Portion of a cross section through the vagina in the region where the musculature reaches its greatest development. × 120.

" 16. Longitudinal section of the wall of one of the smaller pharynges. × 500.

" 17. Portion of a longitudinal section through the slime glands in the head region, where they pass over the brain. × 300.

" 18. Portion of a cross section of the body to show the reticulated mesenchyma and its relation to sagittal muscles. × 500.

" 19 and 19*a*. Portions of the incipient yolk glands; in Figure 19 the nuclei are seen in process of division. × 820.

" 20. A partial reconstruction of the whole worm showing the pharynges and their relation to the intestinal tract. × about 20.

" 20*a*. Outline to show the appearance of the living worm while in progression. × 9.

" 20*b* and 20*c*. Outlines showing forms assumed by the worm when at rest. × 6.

" 21. Longitudinal section through the ovary and parovarium showing their relation to each other. × 300.

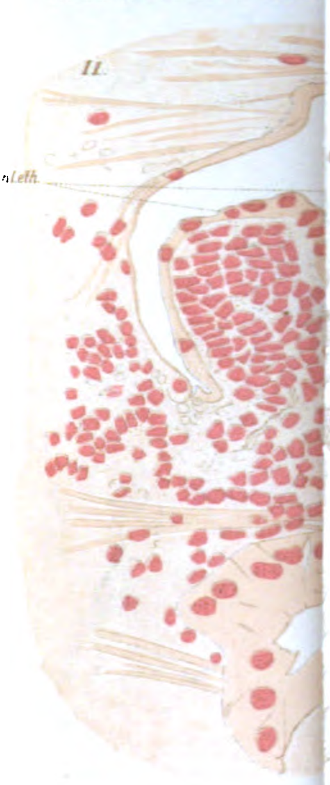
" 22. Section through a parovarium at the time when the yolk glands are beginning to develop. From the same individual as Figures 19 and 19*a*. × 820.

" 23. Cross section through the vas deferens. × 300.

" 24. Portion of a section which passes through one of the testicular sacs, showing its tubular outgrowth, — vas efferens × 300.

WOODWORTH.—PHAGO

11.



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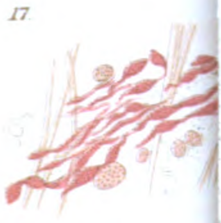

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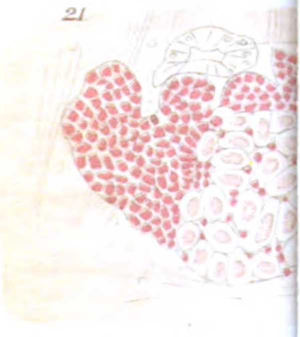

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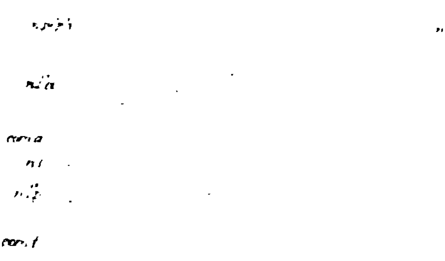
PLATE III.

Fig. 25. Horizontal section through the head region showing the brain and sensory nerves, and the relation of the anterior longitudinal nerve to the marginal nerve (*n. pi'ph.*). The right-hand side of the section is a little more dorsal than the left. × 52.

" 26–31. From a series of cross sections through the brain region. The sections are taken at intervals of 60 μ. Figure 26 is the most anterior. × 52.

" 32–36. From a series of horizontal sections through the brain region, cut from the dorsal side. The sections are consecutive, and 30 μ in thickness. × 52.

25



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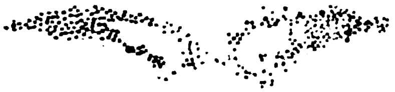

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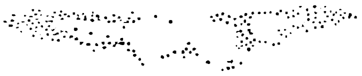

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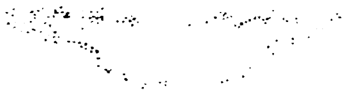

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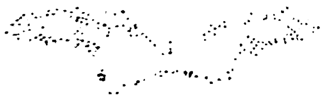

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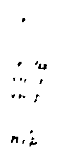

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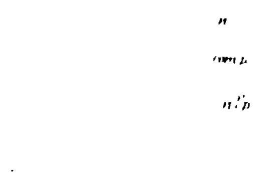

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PLATE IV.

Figs. 37 and 38 Two consecutive horizontal sections (30 μ in thickness) from the ventral side passing through the floor of the pharyngeal chamber. Figure 37 is the more ventral, and shows the marginal nerve; the relation of the latter to the longitudinal trunks is evident upon comparing Figures 37 and 38. × 27.
" 39 and 40. Two longitudinal sections, parallel with the sagittal plane, through the brain region. × 52.
" 41. From an isolation preparation, showing one of the sub-hypodermal glands from the region of the gonopore. × 700.
" 42. A view of the sexual organs showing their relations to one another. The figure was accidentally inverted by the lithographer, thus bringing the posterior end uppermost. Partially diagrammatic. × 35.
" 43. Portion of a cross section of one of the lateral branches of the intestine. × 450.
" 44. Portion of a section through a parovarium of an individual in which the yolk glands were fully developed. × 680.
" 45. Section through a portion of a yolk gland from the same individual as Fig. 44. × 260.
" 46. Sagittal section through the brain, showing the two commissures. × 60.
" 47. Portion of a tangential section of one of the pharynges, to show the cell boundaries of the external epithelium. From an isolated pharynx killed in hot silver nitrate. × 350.

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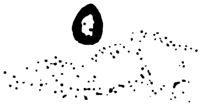

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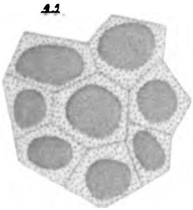

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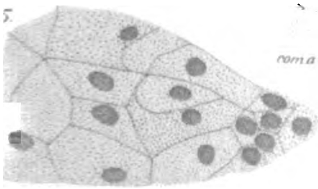

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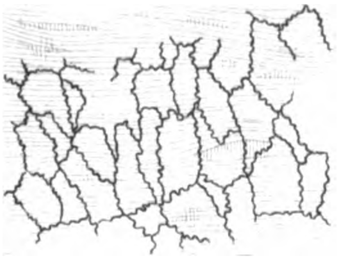

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AT HARVARD COLLEGE.
VOL. XXI. No. 2.

25

THE COMPOUND EYES IN CRUSTACEANS.

BY G. H. PARKER.

WITH TEN PLATES.

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No. 2.—*The Compound Eyes in Crustaceans.* By G. H. Parker.[1]

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Introduction.

Some four years ago, at the suggestion of my instructor, Dr. E. L. Mark, I began the investigation of the compound eyes in Crustaceans. In order to familiarize myself with the subject, I determined to study at first in detail the structure of the eyes in a single species, and for this purpose I turned my attention to our common lobster, Homarus americanus. My results were published in a paper entitled "The Histology and Development of the Eye in the Lobster." Since the publication of that paper, I have had the opportunity of examining the eyes in a number of other Crustaceans, and my observations and conclusions concerning these eyes are contained in the following pages.

The *material* which I have used in the present study was in part supplied to me through the kindness of several friends, and in part collected by myself. Of that which I obtained myself, some was gathered in the immediate vicinity of Cambridge, but much of it came either from Wood's Holl, Mass., or from Newport, R. I. The material which I obtained at Newport was collected at the Newport Marine Laboratory during the summer of 1890, and consisted of specimens of Idotea, Evadne, and Pontella; that which I got at Wood's Holl was collected at the United States Fish Commission Station during a brief period which I spent there in the summer of 1889, and included much the material which I used in studying the eyes of Decapods. For opportunities of collecting, both at Newport and Wood's Holl, I indebted to Dr. Alexander Agassiz. I also desire to express my tha to Prof. M. McDonald, the United States Commissioner of Fish Fisheries, for many courtesies shown me while at the governm station at Wood's Holl.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXV.

Essentially the same *methods* as those which I used in investigat the eyes in the lobster were employed in studying the eyes in ot Crustaceans. As these methods have been described at some lengtl my paper on the lobster's eye (Parker, '90ᵃ, pp. 3, 4), further men of them in this connection is unnecessary.

Before proceeding to an account of the eyes in Crustaceans, a statements should be made concerning the use of terms. In the lowing anatomical descriptions, I have very generally adhered to older and more established terms. It must be admitted that some these, on account of their derivation, are not entirely satisfactory, because of their general acceptance I have chosen to retain them rat than to attempt to replace them by new ones.

The term *retinula*, the use of which varies with different writers, introduced by Grenacher ('77, p. 17), who employed it to designate rhabdome and the group of cells by which this structure is surroun Subsequently, Patten ('86, p. 544) used the same term as a name a single cell of the group to which Grenacher gave the name retin In my paper on the eyes of the lobster I followed Patten's usage, in the present paper I have decided to employ the term as origin defined by Grenacher, and to designate the individual cells in retinula as *retinular cells*, — a translation of the term already used this purpose in many German publications.

The greater part of the present paper is taken up with descript of the eyes in different Crustaceans. The amount of detail thus lected is considerable, and might appear at first sight to include m unimportant particulars; but the number of observations recorde justifiable, I believe, on the ground that the majority of them l more or less directly upon the solution of the principal question d with in the paper.

The following statements will make clear the character of this q tion. It is now well recognized that the retina in compound eye composed of a number of similar units or ommatidia, and that ommatidium consists of a cluster of cells regularly arranged aroun

Vith very few exceptions, the different ommatidia in the
iven Crustacean agree with one another in the number
nt of their cells; in other words, in a given retina any
the structural duplicate of any other. This uniformity
ea of a structural type, and already a number of such
n described. Some of these find representatives appar-
ie ommatidia of a single species, but more frequently the
zes a genus, family, or even a sub-order. Types differ
er, either in the number of their cells or in the arrange-
cells. Of these differences, the one which involves a
e number of cells is the more fundamental. This dif-
er, has probably arisen by the gradual modification of
pe, and, granting this, it follows that the ommatidia of
genetically connected with those of other types. This
the statement of the principal question, namely, *What*
by which ommatidial types are modified, and what is the
he changes through which these types pass?
n, although easily stated, is not so easily answered; the
in the following pages cannot be said to settle it, and
to me to increase materially the possibilities of its

swer to at least the first portion of the question has al-
gested (Parker, '90^{a}, pp. 56–58); it can be briefly stated
ere is reason for believing that those ommatidia which are
mall number of cells more closely resemble the ancestral
composed of many cells. Granting this statement, one
expect that the more complex ommatidia had been de-
simpler ones by an increase in the number of their ele-
s the most natural method by which this increase could
l would be by the further division of the cells already
nmatidium. Consequently, cell division in this sense
to afford a sufficient means for the modification of om-
In the present paper it is in part my purpose to show
t extent cell division can be said to have modified om-
determine whether any other factors have been involved

THE RETINA.

n those Crustaceans in which its development has been
es as a thickening in the superficial ectoderm. At least

three types of retinal structure can be distinguished, depending upon the ultimate form which this thickening assumes.

The FIRST TYPE which will be described is in several particulars the simplest, and probably represents a primitive form from which the other two are derived. This type is characteristic of the eyes in Decapods, Schizopods, Stomatopods, Isopods, the Nebaliæ, and the Branchiopodidæ, and is represented by a simple thickening in the superficial ectoderm.

Branchiopodidæ. — In the eye of adult specimens of Branchipus the retina is a lenticular thickening occupying the inner concavity of the distal end of the optic stalk. Near its edges the retina is directly continuous with the adjoining hypodermis. Its proximal face is bounded by a basement membrane which is also continuous with the corresponding membrane of the hypodermis, and its distal face is closely applied to the inner surface of the superficial cuticula. Thus the retina in the adult has in every respect the appearance of a simple thickening in the hypodermis.

The way in which the retina originates in Branchipus confirms the opinion that this organ has the simple structure suggested in the foregoing paragraph. The development of the retina in this genus has been studied by Claus ('86, p. 309), whose account can be summarized as follows. In that part of the head from which the optic stalks eventually arise, the ectoderm becomes considerably thickened; this thickening is subsequently divided into a superficial and a deep portion; the latter sinks into the head and becomes a part of the central nervous system; the former retains its external position and is converted into the retina. In Branchipus, therefore, the retina originates as a simple ectodermic thickening which retains its superficial position throughout the life of the individual. This method of origin, and the position permanently retained by the retina, are the two principal characteristics of the first retinal type.

Isopoda. — In adult specimens of Idotea irrorata, as sections perpendicular to the external surface of the eye show (Plate V. Fig. 49), the retina bears the same relation to the hypodermis as it does in Branchipus. Similar structural relations occur also in the eyes of Idotea robusta and of young specimens of Serolis Schythei.

The development of the retina in Isopods has been observed by Dohrn and Bullar. As early as 1867, Dohrn ('67, p. 256) described the eye in Asellus as originating in connection with a thickening in the lateral wall of the head, presumably in the ectoderm of that region. The development of this organ were not followed on account of ncrease of pigment. Bullar ('79, pp. 513, 514) in a paper pods described the development of the retina in Cymothoa. substantially as follows. In the course of the developebral ganglion, when this structure is separated from the derm, the latter remains on the exterior of the embryo as derable thickness. From this superficial layer is devel-, i. e. all parts of the eye which in the adult lie between nembrane and the corneal cuticula.

d a few stages in the development of the eyes in Idotea retina in this species originates as a simple thickening in ectoderm, in essentially the same manner as Bullar has nothoa.

ı Isopods, both in respect to its method of development structure in the adult, is unquestionably a representative called the first type of retinal structure.

n Nebalia, as the figures given by Claus ('88, Taf. X. show, the retina and adjoining hypodermis are directly l the former presents all the characteristics of a simple he hypodermis.

— In an adult specimen of Gonodactylus which I exation between retina and hypodermis was the same as in

nown, I believe, of the development of the retina in either the Stomatopods. The structure of the eyes in the adults however, shows very conclusively that their retinas belong uctural type as those of Branchipus.

-In describing the development of Mysis chamelio, Nus-171–185) states that the retina arises from a thickening al ectoderm, and adds that its formation, so far as his tended, was not complicated by an involution.

enolepis, a Schizopod whose eyes I have studied, the odermis in the adult are directly continuous, as in Branelation is what would be expected from the method of scribed by Nusbaum.

Carrière ('85, p. 169), in his account of the eyes in Astary clearly that in the adult the retina and hypodermis uous layer. This relation was subsequently observed by (Parker, '90ª, p. 5), and I have since seen the same consimus, Cardisoma, Cancer, Hippa, Palinurus, Pagurus, Cambarus, Crangon, and Palæmonetes. There is, therefore, considerable ground for the support of Carrière's generalization, that the relation of the retina to the hypodermis as shown in Astacus is characteristic of all Decapods.

The development of the retina has been more fully studied in Decapods, perhaps, than in any other group of Crustaceans. Nevertheless, the accounts given by various writers are by no means in agreement, but differ in several important particulars. In a former paper (Parker, '90^{a}, pp. 31–43), I devoted considerable space to the discussion of these accounts, and I shall therefore not reopen the subject here. Suffice it to say, that since the publication of the paper referred to nothing has transpired to alter my belief that the retina in Decapods originates as a simple thickening in the superficial ectoderm.

In a recent preliminary communication by Lebedinski ('90) on the development of a marine crab, Eriphya, a brief description of the origin of the eye is given. This description, however, is so very much condensed that it is not easily understood, and since the author himself confesses that, on account of the complexity of the subject, a description without figures must be almost unintelligible, it would be unwise to hazard a presentation of his views. I shall therefore pass over this paper without further comment.

The evidence advanced in the course of the preceding paragraphs leaves no doubt in my mind that the retinas in the Branchipodidæ, the Nebaliæ, the Isopods, Stomatopods, Schizopods, and Decapods, belong to the same structural type, and that this type is represented by a thickening in the external ectoderm (hypodermis), which retains permanently its superficial position.

The SECOND RETINAL TYPE is more complicated than the first, and differs from it in that the retina does not retain its position at the surface of the body, but becomes buried beneath a fold of integument. Our knowledge of this type is largely due to the researches of Grobben ('79). The type is represented in the eyes of the Apusidæ, the Estheridæ, and the Cladocera.

Estheridæ. — In adult specimens of Limnadia Agassizii the two lateral eyes are rather closely approximated, and occupy a position in the ventral anterior portion of the animal's body (Plate IV. Fig. 33). The relation of the eye to the surface of the body can be seen most satisfactorily in sagittal sections. In such a section (Fig. 35) the eye has the appearance of a stalked structure which projects anteriorly into a cavity, the optic pocket (*brs. oc.*); this pocket communicates with the

ns of a small opening (*po. brs.*), the optic pore. The
e stalked portion of the eye is covered with a delicate
after being reflected from the base of the stalk over the
the wall of the pocket, becomes continuous at the pore
ith the superficial cuticula. The retina (Fig. 35, *r.*)
ter portion of the optic stalk. Its distal face is bounded
uticula already mentioned, and its proximal face is lim-
nt membrane (*mb. ba.*). This membrane becomes indis-
e of the stalk is approached, but the retina itself is
uuous in this region with the layer of cells which rests
wall of the optic pocket, and which finally unites at the
ket with the superficial hypodermis. Thus the retina
e continuous with the hypodermis.

of the eyes in Limnadia Agassizii is such that they
as stalked eyes which have been surrounded by a fold
nt, so as to become enclosed within a space, the optic
mmunicates with the exterior only by means of the

ntially this structure has been described by Grobben
Limnadia Hermanni, Limnetis brachyurus, and Estheria
the last genus enough of the development of the eye
ndicate that the optic pocket was formed by the growth
gument over the optic stalk.

Apus, according to Grobben ('79, p. 256), the plan of
ally similar to that in the Estheridæ. The eyes pro-
n pocket, the cavity of which permanently communi-
terior. Judging from the figure given by Claus ('86,
, compare p. 366), the right and left retinas in Apus
o one another as in the Estheridæ (compare Plate IV.

he structure and development of the retina in the
een carefully studied by Grobben. My own observa-
up have been limited to a single genus, Evadne, and
ot very favorable for the determination of the general
retina I must rely almost entirely upon Grobben's

ment of Moina, according to Grobben ('79, p. 253), the
g is covered by a fold of the integnment in such a
pen optic pocket is produced, as in Limnadia. By the
corresponds to the optic pore, this pocket eventually

loses its connection with the exterior, and becomes reduced to a clo sac on the distal face of the retina. With the closure of the sac, continuity of the retina with the superficial hypodermis becomes terrupted.

In other Cladocera, especially the genera Sida and Daphnia, Grobl has found evidence to believe that the eyes are of essentially the sa structure as in Moina. In a majority of the Cladocera the two co pound eyes coalesce even more completely than in Limnadia.

In the development of Moina, as the preceding description indicat the eye passes through a phase which closely resembles the perman condition in Limnadia. The eye in the latter may therefore be int preted as representing a stage in the phylogeny of the eye in Moina.

In accordance with the facts presented in the foregoing account, second retinal type can be described as one in which the retina does retain its primitive external position, but sinks below the surface of animal and becomes covered by a fold of the integument. The op pocket thus formed may remain permanently open, as in the Apusi and Estheridæ, or may become closed and partially obliterated, as the Cladocera. The right and left retinas either remain separated, as the Apusidæ, or become closely approximated, as in the Estheridæ, fused, as in the Cladocera.

The minor modifications which this retinal type presents are not wi out importance. Bearing in mind the general statement that the co pound eyes in Crustaceans are separate, paired, superficial structures is evident that the eyes in the Apusidæ, in which the retinas are se rate and the optic pocket permanently open, depart only slightly fr the primitive condition. In the Estheridæ, in which the two reti are closely approximated, the eye is farther removed from the origi type; but not so far as in the Cladocera, in which not only the t retinas are fused, but the optic pocket is closed and partially obliterat thus entirely disconnecting the retina from the hypodermis. The th groups — the Apusidæ, the Estheridæ, and the Cladocera — may c sequently be taken to represent a series in the differentiation of second retinal type. That this series is a natural one, and that it c minates in the Cladocera, is shown from the fact that in the devel ment of Moina, and perhaps many other Cladocera, the eyes p through stages which reproduce the essential features of the perm nent condition in the Apusidæ and Estheridæ.

In the THIRD RETINAL TYPE, as in the more differentiated form the second, the retina is completely separated from the hypoderm which the separation is here accomplished is not by involution, as in the second type, but by a process iich will be described in the following pages. The resented by the eyes in Amphipods, and possibly in

The peculiar relation which the retina bears to the mphipods can be easily seen in Gammarus. In this re ('85, pp. 156–160) has clearly demonstrated, the iately below the hypodermis, and is separated from the defined structure, the corneo-conal membrane (Fig. 1, is membrane, although visible with perfect clearness, xtremely delicate, and has the appearance of a single ve, however, that its structure is more complex, and sed of two very intimately united membranes, one of by the retina, the other by the corneal hypodermis. ed upon the fact that at the edge of the retina the membrane separates into what may be considered its One of these becomes the basement membrane of dermis, and the other, which I have called the cap- passes over the edge and proximal face of the retina, lected over the optic nerve (Fig. 1, *mb. n. opt.*). In capsular membrane, the eye in Gammarus possesses nbrane (Fig. 1, *mb. ba.*). This is a delicate lamella, ately parallel to the deep face of the eye at a level lomes and retinular nuclei (compare Fig. 2), and which les the space within the capsular membrane into two distal and a smaller proximal one. At its periphery nembrane unites with the capsular membrane.

al and capsular membranes in Gammarus show no evi- forated, but together constitute a closed capsule, which ina from all adjoining tissues except the optic nerve. are composed apparently of a homogeneous substance, never been able to distinguish any trace of cells. It ble that these membranes are cuticular.

g membrane, unlike either the capsular or the corneo- is pierced by a great number of holes, through which of the retinular cells project. This membrane, there- of a meshwork. According to Carrière ('85, p. 158) numerous connective-tissue cells, but this statement by my own observations. In depigmented sections of the retina the intercepting membrane had the appearance of a delica lamella, in which I was unable to find any trace of cells. Not unfr quently the nuclei of certain accessory pigment cells (Fig. 2, *nl. h'drm* appear to touch the membrane, and even at times to lie with their lo axes parallel to it, but in no case could these nuclei be said to be *in* t membrane. In sections of the retina from which the natural pigme had not been removed, it was often difficult to decide whether a giv nucleus was *in* the membrane or only *next to* it. Possibly appearanc such as these have led Carrière to believe that the membrane was c lular. My own opinion is, that the intercepting membrane, like t other two membranes, is a cuticula, and does not contain cells.

From the foregoing account, it will be seen that in an adult Gammar the retina lies immediately under an undifferentiated corneal hypode mis, and is enclosed, excepting where the optic nerve emerges from by a non-perforated cuticular capsule. The space within this capsu is divided by a perforated cuticular membrane into a large distal and small proximal chamber.

In Hyperia, judging from the figure given by Carrière ('85, p. 16 Fig. 123), the retina has essentially the same structure as in Gammaru The intercepting membrane is in a position proximal to the rhabdom and distal to the retinular nuclei. The layer of pigment cells, whi Carrière ('85, p. 161, Fig. 124) apparently considers the intercellul membrane itself, in my opinion marks only approximately the positi of that membrane. Probably in Hyperia, as in Gammarus, these cel rest on the distal face of the intercepting membrane.

In Phronima each side of the head is occupied by two eyes, instead one, contrary to the condition in the more typical Amphipods. Of t two eyes, one is dorsal, the other lateral. This difference in positi affords a convenient means of distinguishing them. The lateral eye pr sents all the essential structural features of the single eye in Gammar (compare Carrière, '85, Figs. 125 and 121). The dorsal eye, althoug differing considerably in shape from the lateral one, is nevertheless co structed upon the same morphological plan. Its most important pec liarity is the shape of its intercepting membrane and the adjoini structures. In the dorsal eye the intercepting membrane, instead lying in a plane nearly parallel with the external surface of the retin as in the lateral eye, is cone-shaped. The axis of this cone correspon to the axis of the eye; its apex is near the brain, and its base faces t external surface of the eye (compare Claus, '79, Taf. III. Fig. 20, ar Taf. VII. Fig. 58). The ommatidia are arranged approximately parall

axis ; distally, they terminate in the region of its base ;
end either at its apex or on its lateral walls near the
domes lie within the cavity of the cone, i. e. they are
rcepting membrane, as in other Amphipods. The retin-
the apical portion of the external surface of the cone,
ximal to this membrane. These nuclei are covered ex-
ond cone-shaped membrane, which separates them from
tissue. This membrane occupies the position of the cap-
of other Amphipods, and is unquestionably homologous

both the lateral and dorsal eyes in Phronima are con-
he same plan as the single eye in Gammarus, supports
se two eyes have arisen by the division of a primitively
two parts, and the subsequent independent differentia-
t.

ing account shows, in all Amphipods whose eyes have
efully, the retinas conform to one structural type well
ammarus. In this type the retina is characterized by
: first, it is not continuous with the hypodermis, but
below that layer ; and secondly, it possesses what appear
ent membranes, the capsular and the intercepting mem-
gnificance of these peculiarities will be discussed in the
aphs.

n of the retina from the hypodermis is characteristic of
ture conditions of the eye in Amphipods ; for as Pereyas-
202) has shown in Gammarus, and Rossiiskaya ('89,
p. 89) has demonstrated in Orchestia and Sunamphitoë,
ates as a thickening in the superficial ectoderm, in the
in the majority of Crustaceans. So far as I am aware,
has observed the detachment of the retina from the
rocess which must take place before the adult condition
the figure of the developing eye in Gammarus given by
('88, Plate VI. Fig. 120), the distal portion of the retinal
ins almost nothing but developing cones. In sections of
corresponding region in a young specimen of Gammarus,
n of the retina contains not only developing cones, but
lei, which occasionally lie between the cones, but more
in positions distal to them. These nuclei are as numer-
e of the distal face of the retina as on its edges, and at
ways be easily distinguished from the nuclei of the cone

cells. I believe they represent the nuclei of the corneal hypoder The retina proper is probably separated from this hypodermis by dela nation ; at least, the corneo-conal membrane is formed at a stage sligh older than that last mentioned, and, judging from the appearance this stage, its formation is not accompanied by any folding of the hy dermis or retina, but is the result of a differentiation in place. Ur tunately, none of the specimens which I studied showed any steps in formation of the corneo-conal membrane, and I am therefore uncertai to the exact method of its growth.

Of the two membranes in the basal portion of the retina of Gamma presumably only one corresponds to the basement membrane of ot Crustaceans. The position occupied by the two membranes, as wel their structure, serves to indicate which is the true basement membra At first sight one might suppose that the capsular membrane, at l in its proximal portion, corresponds to the basement membrane, but interpretation is not probable, for the reason that the capsular m brane is not pierced by the fibres of the optic nerve, a characteristi the true basement membrane of the eye. I therefore believe that intercepting membrane, since it is perforated by these fibres, is the ho logue of the basement membrane, and that that portion of the caps membrane which might be regarded as a basement membrane i reality merely the cuticular sheath of the optic nerve.

So far as I can foresee, the only objection to be urged against interpretation of the intercepting membrane is found in its relation the retinular nuclei. These nuclei in the eyes of almost all other Cru ceans lie on the *distal* side of the basement membrane. Granting t the intercepting membrane is the basement membrane, one must ad that in Amphipods they lie on the *proximal* side of this membra This admission might at first sight appear to offer an obstacle to homology which I have suggested ; but it can be made with consiste I believe, provided one can show that the position of the retinular nu is not necessarily fixed. That such is the case is evident from the lowing facts. In Decapods the retinular nuclei usually occupy a posi in their cells distal to the rhabdome. In Porcellio, as Grenacher (Taf. IX. Fig. 96) has shown, they have a more proximal position, l in the same transverse plane as the rhabdome itself. In Serolis t are midway between the rhabdome and the basement membrane. Th conditions show, I believe, that the retinular nuclei may occupy v different positions in their cells, and that the step from the condi shown in Decapods to that shown in Serolis is not greater than t he Amphipods. It seems to me, therefore, that the d at the beginning of this paragraph is almost without nclusion, moreover, is supported by the fact that in Fig. 49) the retinular nuclei lie proximal to the basewhereas in the majority of other Isopods they are mbrane.

ding discussion, I conclude that the retina in Amphi- a simple thickening in the superficial ectoderm, and ng subsequently becomes separated, probably by a proion, into a deeper portion, the retina proper, and a portion, the corneal hypodermis. The latter alone reconnection with the adjacent hypodermis. Of the two t in the basal portion of the eye in Amphipods, that ed the intercepting membrane is homologous with the ne of the retina in other Crustaceans, and that which ted as the capsular membrane is in large part the of the optic nerve.

e retinas in the Branchiura and Eucopepoda, the two Copepods, present such different structural conditions of description it is better to consider them separately. In adult specimens of Argulus, the retina is completely surrounding tissue, excepting the optic nerve, by an space (Plate II. Fig. 11, *cœl.*). This peculiar condily described by Leydig ('50, p. 331), although as early 6, p. 447) remarked that the eye in this genus was nsparent membranous sac, which apparently contained ('31, p. 97) some twenty-five years later described the d from the "cornea" by an intervening space filled mained, however, for Leydig to determine the extent to demonstrate that the fluid which it contained was essential features of Leydig's description have since Claus ('75, pp. 254–256).

nt of the eye in Argulus has not been studied with o allow one to determine the relation of its retina to But from the strong resemblance which the eye in the at in Amphipods, it is probable that the course of he two cases is not unlike. Probably the retina in as a thickening in the superficial ectoderm, and subseuffers delamination, as in the Amphipods, but becomes n from the superficial layer (corneal hypodermis).

If this course of development really takes place, the various struct
in the eye of an adult Argulus can be easily homologized with t
in Amphipods. Thus the corneal hypodermis and corneal cuticul
Amphipods would probably be represented by the hypodermis and
ticula dorsal to the eye in Argulus (Fig. 11). The basement m
brane of this hypodermis would correspond to the corneal compo
of the corneo-conal membrane of Amphipods, and the conal constitu
would be represented by what is called the preconal membrane in A
lus (Fig. 11, *mb. pr'con.*). Proximally, the preconal membrane beco
continuous with the sheath of the optic nerve (Fig. 11, *mb. n. o*
the equivalent of the capsular membrane of Amphipods. The basem
membrane of the retina in Argulus, as in Amphipods, is the membr
pierced by the fibres of the optic nerve (Fig. 11, *mb. ba.*).

Grobben ('79, p. 258) has suggested that possibly the eye in Arg
is of the same type of structure as in Phyllopods, but I do not sl
in this opinion for the following reasons. In Estheria, the deli
cuticula which covers the optic stalk is morphologically a portio
the outer surface of the body, and, as I hope to show subsequentl
subtended by a true corneal hypodermis. There is no corneal h
dermis beneath the preconal membrane of Argulus. Moreover, t
is nothing in the eye of Argulus to correspond to the optic pocke
the Estheridæ, or to the optic sac of the Cladocera, except the circ
retinal blood space, and it seems to me very improbable that this s
was once a cavity in communication with the exterior, and afterw
became converted into a blood space. I therefore believe that
plan of the eye in Argulus is not similar to that in the Phyllop
but rather that it represents a modification of the type presented
the Amphipods. The satisfactory determination of this question
be settled, however, only by embryological evidence.

Eucopepoda. — In adult specimens of those true Copepods w
possess rudiments of the lateral eyes, — the Pontellidæ and Corycæi
— the retina is apparently separated from the hypodermis. In
Corycæidæ it usually lies at some considerable distance from the h
dermis, and in Pontella the two structures, although near one anot
are nevertheless not continuous.

The development of the lateral eyes in the Corycæidæ and Pon
lidæ has not been studied, and consequently it cannot be stated w
certainty whether the retinas in these Crustaceans originate from
hypodermis or not. In the metanauplius larva of Cetochilus, a Cope
which as an adult has no lateral eyes, Grobben ('80, p. 262) has

of thickenings, which extend from the superficial ectoderm ateral part of the head to the brain. These thickenings ly in the early stages of development, and represent the nection between the brain and the superficial ectoderm. esemble the developing lateral eyes of Branchipus, and therefore very justly considered them rudiments of the If the rudiments of the lateral eyes in Cetochilus de- superficial ectoderm, it is probable that the lateral eyes ods have a similar origin.

f the three retinal types already described the eyes in ng is not easily decided. The absence of any indication ocket, either in the development of what Grobben con- ments of the lateral eyes in Cetochilus, or in the fully other genera, seems to me to preclude the possibility of longing to what I have described as the second type. of the retina from the hypodermis prevents them from with the first type, and, especially in the case of the ings them into close relation with the third type. It is at, if the lateral eyes in Copepods are not representatives e, essentially different from the three already described, onsidered members of the third retinal type.

ies of Cumaceæ, Ostracods, and Cirripeds possess optic probably represent the compound eyes of other Crusta- far as I am aware, the relation of these structures to the unknown. It is therefore impossible to state whether esent other retinal types, or belong to one of the three ed.

o the preceding account, three retinal types can be dis- he compound eyes of Crustaceans. In the first of these a simple thickening in the superficial ectoderm (hypo- type is characteristic of the eyes in Isopods, the Bran- e Nebaliæ, Stomatopods, Schizopods, and Decapods. In e eyes are sessile; in the other groups of the first type, on the distal ends of movable optic stalks.

d type, although the retina, as in the first type, originates in the superficial ectoderm, it ultimately becomes en- n optic pocket. This may remain permanently open, as æ and Estheridæ, or it may become closed, as in the the Apusidæ, so far as I am aware, the eyes are not capable of motion, and in the Estheridæ they are, if at all, only slightl movable. In the Cladocera, where the second type probably reaches it greatest differentiation, the retina is remarkable for the freedom of it motion.

In the third type the retina originates from thickened hypodermi which subsequently separates into two layers, the corneal hypoderm and the retina proper (a layer of cones and retinulæ). This separatio is accomplished either by the formation of a corneo-conal membrane, in Amphipods, or by what I believe to be an actual withdrawal of th retina proper from contact with the hypodermis, as in Copepods. Onl in the representatives of the extreme modification of this type, the Cop pods, are the eyes movable.

The course of development taken by each of the three types ve clearly indicates their mutual relations. Evidently the first type is primitive one, and since the first steps in the development of the secon and third reproduce the permanent condition of the first, these two ma therefore be considered derivatives from the first. It is interesting observe that in the simpler condition of each type the retina is fixe whereas in the more differentiated form it has become movable. Th sinking of the retina into the deeper parts of the body, as represented the second and third types, may have been induced by the protectio thus obtained for the eye. After the three types were differentiate each one seems to have been modified in a special way to give rise to movable retina.

ARRANGEMENT OF THE OMMATIDIA.

The ommatidia in the retinas of some Crustaceans are so few in nu ber that they can scarcely be said to be grouped according to any syste Where they are numerous, however, they are arranged upon one or t other of two plans. These may be designated the hexagonal and tetrag nal plans of arrangement. In the hexagonal plan the imaginary outli of the transverse section of an ommatidium is a hexagon, and ea ommatidium, excepting those on the edge of the retina, is surrounded six others. In the tetragonal arrangement the ideal transverse sectio of an ommatidium is a square. Each of the four sides of this squa is occupied by one of the four faces of an adjoining ommatidium.

The arrangement of the ommatidia can usually be determined a careful inspection of the external surface of the eye; this determin tion is considerably facilitated by the presence of a facetted cuticl Sometimes the form of a single facet is sufficient to indicate the plan

hus, hexagonal facets have never been observed except
h the hexagonal plan of arrangement. Circular facets
yn to occur only with this method of grouping. Square
her hand, may accompany either the hexagonal or te-
nent of deeper parts.

arrangement is apparently characteristic of the om-
-ustaceans,[1] except the Decapods. In the Decapods, as
sently, the ommatidia are arranged either upon the hex-
ragonal plan. Before proceeding, however, to a descrip-
gement of the ommatidia in Decapods, it would be well
tention to the rather peculiar grouping of these struc-
tylus, a Stomatopod.

nderstanding of the arrangement of the ommatidia in
it is necessary to have some previous knowledge of the
stalk. In Gonodactylus the stalks are elongated cyl-
l ends of which are rounded. In alcoholic specimens
undisturbed position rest with their longitudinal axes
rallel with the chief axis of the animal, and with their
ted forward. The retina occupies the free end of the
it extends over the distal half, ventrally over only the
stalk.

in Gonodactylus are of two kinds, large and small,
easily distinguishable from each other, although they
ial respect except size. The large ommatidia are defi-
in six rows, which extend as well defined bands from
or edge of the retina anteriorly over its rounded distal
rly over its ventral surface to its ventral posterior edge.
ccupies both dorsally and ventrally the median portion

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the figures as well as the statements made by the authors
ial arrangement is characteristic of the ommatidia in the fol-
(exclusive of the Decapods): *Branchipus* (Burmeister, '35,
g, '75, p. 30), *Nebalia* (Claus, '89, Taf. X. Fig. 10), *Gammarus*
rchestia (Frey und Leuckart, '47, p. 204), *Phronima* (Claus, '79,
Cymothoa (Müller, '29, Tab III. Figs. 5, 6, Bullar, '79, p. 514),
et, '43, p. 107, Planche 4, Fig. 2^b), *Serolis* (Owen, '43, p. 174),
'90, Plate XXXI. Fig. 4), *Anceus* (Hesse, '58, pp. 100 and 103,
II. Figs. 33, 34), *Squilla* (Milne-Edwards, '34, p. 117, Will, '40,
ickart, '47, p. 204, Leydig, '55, p. 411), and *Mysis* (Sars, '67,
Grenacher, '79, Taf. X. Fig. 112). I have observed the hexag-
n the following genera: *Apus*, *Branchipus*, *Estheria*, *Evadne*,
, *Caprella*, *Talorchestia*, *Idotea*, *Serolis*, *Porcellio*, *Sphæroma*,
ctylus.

of the retina, and separates the remaining retinal surface into two parts, one on either side of the stalk. In alcoholic specimens this median band is readily visible with the aid of a hand lens, and a little closer scrutiny shows that it is composed of six lines. These lines, of course, correspond to the six rows of ommatidia previously mentioned. The smaller ommatidia, on either side of the median band, are also arranged in lines parallel to those in the band; but, on account of their smaller size, the lines formed by them are not visible with an ordinary lens.

The smaller ommatidia in Goniodactylus are arranged upon the typical hexagonal plan (see the left half of Fig. 93, Plate VIII.). The larger ones have a somewhat similar grouping, although the fact that they are in six longitudinal rows rather obscures their hexagonal arrangement. (See the right half of Figure 93, in which three rows, and a part of a fourth, of large ommatidia are shown.) The hexagonal arrangement is not disturbed, as might be expected, on the line which separates the larger from the smaller ommatidia, but both kinds form parts in a common system. That this is true can be seen from Figure 93, where it will be observed that the *centres* of any two small ommatidia lying in the same vertical line are as far apart as the *centres* of the corresponding larger ommatidia. Moreover, as I have demonstrated by actually counting the ommatidia of long parallel series, a vertical band which contains twenty-five large ommatidia has the same length as one composed of a corresponding number of small ones. The apparent difference in numbers at first sight presented by lines of the two kinds of ommatidia is principally due to the fact that the larger ommatidia are arranged in distinct rows, whereas the smaller ommatidia are so grouped that the individuals in one row are slightly interpolated between those of the two adjoining rows (compare Fig. 93).

In Decapods the ommatidia are arranged either upon the hexagonal or tetragonal plan. In the Brachyura,[1] as well as in three families of the Macrura, the Hippidæ, Paguridæ, and Thalassinidæ,[2] the arrangement

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[1] The presence of hexagonal facets has been recorded in the following genera of Brachyura: *Portunus* (Will, '40, p. 7); *Ilia* (Will, '40, p 7, Leydig, '55, p. 411); *Cancer; Maja; Carpilius* (Frey und Leuckart, '47, p. 204): *Herbstia*, *Dorippe*, and *Lambrus* (Leydig, '55, pp. 407, 410, and 411, respectively). This form of facet is present only when the ommatidia are hexagonally arranged. Leydig ('55, p. 411) states that the outline of each facet in *Dromia Rumphii* is square, but, as his description clearly indicates, the facets are arranged upon the hexagonal plan. As my own observations show, the ommatidia in *Cardisoma Guanhumi*, Latr., *Cancer irroratus*, Say, and *Gelasimus pugilator*, Latr., are hexagonally grouped.

[2] The outline of the corneal facets is stated to be hexagonal in the following genera: *Pagurus* (Swammerdam, '52, p. 88, Cavolini, '92, p. 130, Milne-Edwards,

is invariably hexagonal. In the remaining macrurous
nmatidia are grouped on the tetragonal plan. This last
ver, is not without exceptions, for in Typton, and at
athea,[2] the hexagonal arrangement appears to prevail.
of these exceptions will be offered in a subsequent

ting this explanation, however, it will be well to gain a
e relation of the hexagonal and tetragonal methods of
t first sight, it might appear that these two methods
relations, and were simply characteristic of different
, however, is not the case; for, as the development of
, the ommatidia in a *single* animal can be arranged at
one plan, and afterward according to the other. In
hexagonal arrangement characterizes the earlier stages
and is replaced only subsequently by the tetragonal
nilar change also occurs in the spiny lobster. Thus,
ne larva of either Palinurus or Scyllarus, the hexagonal
by Milne-Edwards ('34, p. 115) afford unquestionable
exagonal arrangement at this stage. In the adult con-
both of Palinurus and of Scyllarus, according to my own
ommatidia are tetragonally grouped. In the common
spiny lobster, then, the hexagonal arrangement of the
placed by the tetragonal one in the adult. These ob-

40, p. 7, Frey und Leuckart, '47, p. 204, Chatin, '78, p. 8);
Gebbia (Milne-Edwards, '34, p. 117). In *Pagurus longicarpus*,
lpoida, Say, I have observed a hexagonal arrangement of the

he figures given by various authors, the ommatidia of the fol-
characterized by the tetragonal arrangement: *Galathea* (Will,
Astacus (Müller, '26, Tab. VII. Fig. 13, Leydig, '57, p. 252,
ach, '86, Taf. XIV. Fig. 226, Huxley, '57, p. 353); *Homarus*
XVI. Fig. 3, Parker, '90[a], p. 8); *Palæmon* (Grenacher, '79,
, Patten, '86, Plate 31, Fig. 115); *Penæus* (Patten, '86, Plate
y present observations have shown, the tetragonal arrangement
the ommatidia in *Palinurus Argus*, Gray, *Cambarus Bartonii*,
garis, Say.

Chatin ('78, p 13) the outline of the facet in *Typton* is hexagonal.
angement of the ommatidia in this genus is upon the hexagonal
according to the figures given by Patten ('86, Plate 31, Fig.
are hexagonally arranged, although it must be borne in mind
. III. c.) figure of the facets in *Galathea strigosa* affords unmis-
a tetragonal arrangement.

servations appear to me to afford considerable evidence in favor of the view that the hexagonal arrangement is phylogenetically more primitive than the tetragonal.

Granting this conclusion, a number of otherwise exceptional observations can be explained. Thus, as long ago as 1840, Will ('40, p. 7) called attention to the fact that in Astacus, where the ommatidia are normally arranged upon the tetragonal plan, facets near the edge of the retina are often irregularly hexagonal. The edge of the retina is well known to be the last part produced, and therefore it is probably the part least differentiated. Admitting the hexagonal arrangement to be a primitive one, it is only natural to expect that, if it persists at all, it will persist in the less modified portion of the retina. Hexagonal facets also occur on the periphery of the retina in Homarus, and are to be explained, I believe, in the same way.

On the assumption that the hexagonal plan is primitive, the occurrence of a few genera with ommatidia hexagonally arranged, in a group in which the tetragonal arrangement is the rule, can also be explained. In Typton, for instance, the hexagonal plan obtains, although in almost all Crustaceans closely related to it the tetragonal system prevails. This condition may be explained, however, by the fact that the eyes in Typton show evident signs of degeneracy, due in all probability to the parasitic habits of the Crustacean. If the hexagonal arrangement represents an early ontogenetic phase in the development of Decapods related to Typton, it would be natural to expect that in Typton itself, where the normal development of the eyes is interrupted by parasitism, this arrangement would persist permanently.

In Galathea, as I have already mentioned in a note on page 63, the ommatidia according to Will are arranged tetragonally; according to Patten, hexagonally. At first sight these observations might appear to be irreconcilable, but such is not necessarily the case. So far as I have been able to ascertain, Patten does not mention the name of the species which he studied. Possibly he may have examined some other than G. strigosa, the one from which Will's figures were drawn. In such an event, a difference in the arrangement of the ommatidia may have been characteristic of the two species, although, if both possessed well developed eyes, this difference would be somewhat anomalous. If this is not the true explanation, it is still possible that the specimens studied by Patten were somewhat immature, in which case the hexagonal arrangement might very naturally be present. From what has been said, I think it must be evident that the apparent contradiction in Will's and

ents is not so serious as might at first be supposed, and
he relations already mentioned between the two plans
the observations of these two writers can be explained
ng either of them to be wrong.
method of rearrangement by which the hexagonal plan
the tetragonal has been suggested in a previous paper
50). It involves two changes: the conversion of the
e of the ommatidium, as seen in the corneal facet, into
d the slipping of the rows of ommatidia one on the other,
s which bound the four sides of each facet finally form
es of lines which cross each other at right angles.
omewhat intermediate between the hexagonal and tetrag-
t is shown in the retina of Crangon (Plate X. Fig. 123).
he outlines of the ommatidia as seen in the facets are
their arrangement suggests the hexagonal type. The
ping of the ommatidia in Crangon represents a stage
ice of the condition seen in some young lobsters (com-
0^{a}, Plate IV. Fig. 55), and the particular features in
nce is shown are two. First, the distal retinular nuclei
123) are grouped in pairs, more as they are in adult
ot in circles of six, as in young ones (compare Parker,
d 55). Secondly, the arrangement of the ommatidial
nce to the hexagonal plan is more symmetrical in the
han in Crangon, where the rows of ommatidia have ap-
somewhat upon one another so as to resemble more
ition in the adult lobster.
unable to determine with certainty what occasions the
hexagonal to the tetragonal arrangement. Apparently
n excessive growth on the part of the individual omma-
bster, for instance, the ommatidia rearrange themselves
es when the young animal is one inch and eight inches
this period the ommatidia increase about ten times in
ut five times in breadth. The increase is especially
eir distal ends, and particularly in the cone cells. In
of one inch in length (Parker, '90^{a}, Plate IV. Fig. 55),
en the cones of adjoining ommatidia is considerable; in
ortionally very much less (compare Parker, '90^{a}, Plate I.
cones are crowded against one another. Under these
hexagonal arrangement apparently gives way to the te-
r as I am aware, the tetragonal arrangement occurs only

in connection with this crowding of the cones, a condition found for the most part only in macrurous Decapods.

In accounting for the rearrangement of the ommatidia, the eyes in the Stomatopod Gonodactylus afford some important evidence. As I have previously mentioned, the ommatidia in this genus are of two sizes. The larger ones have several of the peculiarities characterizing the tetragonal arrangement: their facets are generally square; they are arranged in single lines, and these lines, so far as the relations of the individual ommatidia are concerned, show evidences of having slipped upon one another. The smaller ommatidia have hexagonal facets, and are clearly arranged according to the hexagonal plan. The larger ommatidia are rather closely packed; the smaller ones are arranged with more open space between them (compare Plate VIII. Fig. 93). In this genus, then, as in the lobster, the tetragonal arrangement occurs in connection with the crowding of the ommatidia.

How an increase in size, accompanied by a crowding of the retinal elements, can induce the change in arrangement which seems to follow it, I am at a loss to explain. Nevertheless, the two phenomena appear to be in some way connected.

From the preceding discussion concerning the arrangement of the ommatidia, the following conclusions can be drawn. The ommatidia, when numerous enough, present one of two plans of arrangement, the hexagonal or the tetragonal. The hexagonal plan is phylogenetically the older, and is characteristic of the eyes of all Crustaceans except some families of the macrurous Decapods, especially the Galatheidæ, Palinuridæ, Astacidæ, and Carididæ. In these the hexagonal arrangement is usually replaced by the tetragonal; but in the adults of some species, especially those in which the eyes are partially rudimentary, the hexagonal arrangement persists. The change from the hexagonal to the tetragonal arrangement is connected apparently with an increase in size, and consequent crowding, of the ommatidia.

THE STRUCTURE OF THE OMMATIDIA.

Each ommatidium, as I have previously mentioned, consists of a cluster of cells more or less regularly arranged about a central axis. The greatest number of kinds of cells which an ommatidium is known to contain is five. These are the cells of the corneal hypodermis, the cone cells, the proximal and distal retinular cells, and the accessory cells.

he corneal hypodermis are usually arranged in a very
constitute the most superficial tissue in the retina.
ent no definite arrangement, as in Amphipods, or they
ouped in pairs, one pair for each ommatidium, as in
Crustaceans. On their external faces they produce the
This is unfacetted in those Crustaceans in which the
not regularly arranged and facetted when they are
s.

s in each ommatidium are united to form the cone, a
which extends from the corneal hypodermis proximally
matidium at least as far as the rhabdome. The cone
s of the distal portion of the ommatidium.

retinular cells are usually limited to the proximal por-
matidium. They are definitely arranged around the
of that region, the rhabdome, and together with it form
he retinula. The optic nerve fibres terminate in the
lar cells.

inular cells are present in only the more differentiated
ey are two in number, and invest the sides of the cone
ne at which this structure emerges from the retinula.
s are present, the remaining cells of the retinula will be
proximal cells; when the distal cells are wanting, the
be called simply retinular cells.

cells fill the space between the elements of an omma-
een separate ommatidia. Their number is apparently
they present a variety of forms. They may or may
nent. Depending upon their source, two kinds can be
ctodermic and mesodermic.

the ommatidia, I shall consider them according to the
aceans in which they occur. Under each group the
ising the ommatidium will be described in the order
ave just been mentioned.

the following account is to determine, as far as possible,
nt kinds of ommatidial types are, and to define these
statement of the number and kinds of cells which char-

es are known to occur in some Ostracods, and in the
Cirripeds, but their histological structure, I believe, has
lied. I am therefore compelled to dismiss these two
further comment, and proceed with the description of

the ommatidia in other Crustaceans. The order in which the grou will be considered is one which is intended to emphasize their relatio only in so far as the structure of their ommatidia is concerned. Nat rally, this order will vary somewhat from the one usually given in sy tematic treatises. I shall begin with the Amphipods.

Amphipoda.

Within recent years the more important types of eyes in the Amph pods have been studied with such care that the structure of their or matidia is perhaps better known than that of any other large group Crustaceans. My own observations do little more than confirm tl accounts already published.

The species of Amphipods whose eyes I have examined are Gammar ornatus, M. Edw., Talorchestia longicornis, Say, and an undetermine species of Caprella. Of these the specimens of Gammarus and Caprel were collected at Nahant, Mass., where I also obtained several sets eggs representing stages in the development of the former. Exampl of Talorchestia were kindly supplied me from the collections in tl Museum.

The *corneal hypodermis* in Amphipods was first satisfactorily describe by Claus ('79, p. 131) in his account of the eyes in Phronima. It represented in this genus by a layer of undifferentiated cells lying b tween the corneal cuticula and the membrane which limits the dist ends of the cone cells. A corneal hypodermis similar to that in Phr nima has likewise been described by Mayer ('82, p. 122) in Caprella ar Protella, by Carrière ('85, p. 156) in Gammarus, by Claus ('87, p. 15) the Platyscelidæ, by Della Valle ('88, p. 94) in the Ampeliscidæ, ar by Watase ('90, p. 295) in Talorchestia. I have also identified this stru ture in Gammarus, Caprella, and Talorchestia.

In Gammarus, as Carrière ('85, p. 156, Fig. 121) has clearly show the corneal hypodermis at the edges of the retina is directly continuou with the general hypodermis. According to my own observations th condition is not only met with in Gammarus, but also in Caprella ar Talorchestia.

In Phronima, according to Claus's figures ('79, Taf. VI. Figs. 48 ar 49, *Ma Z.*), the arrangement of the cells in the corneal hypoderm bears no definite relation to the subjacent cones; the distal end of ea cone presents an area which is covered by about a dozen hypoderm cells. In Gammarus I have observed (Plate I. Figs. 2 and 3) an esse tially similar distribution of the hypodermal cells; as in Phronima, tl

which cover the area of each cone is about twelve. A
rmis of this same character also occurs in Talorchestia,
s instance the number of cells over a cone is only about

Watase ('90, p. 295), in the species of Talorchestia
ed there were only two cells in the corneal hypodermis
one, or, as he expresses it, under each facet. When com-
results recorded in the preceding paragraph, this observa-
newhat striking, and the more so since two, the number of
s the usual number found under each facet in other Crus-
atase's observation be correct, the relation which would
hed between this Amphipod and other Crustaceans would
g one. The desirability of confirming Watase's observation
be evident; but unfortunately he has not given the name
of Talorchestia which he studied, and I have therefore
o verify his statement. In the only species of this ge-
ve examined, viz. T. longicornis, the arrangement of the
neal hypodermis is very different from that described

ns which I draw from the preceding account are, that
mphipods a corneal hypodermis is present, and the cells
usually not arranged with regularity.
bodies observed by Schmidt ('78, p. 5) in the membrane
neal hypodermis and the retina proper in Phronima, and
laus ('79, Taf. VI. Figs. 48, 49, *B. nu.*) as nuclei, are
represented in other Amphipods. Their significance is
f doubt.
uticula in Amphipods has been described by almost all
facetted.[1] According to Della Valle ('88, p. 94), how-
f the Ampeliscidæ this cuticula is facetted, and Watase
s also observed facets in Talorchestia. But with these
the corneal cuticula of Amphipods has been described

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corneal cuticula has been recorded in the following genera of
hithoe (Milne-Edwards, '34, p. 116); *Caprella* (Frey und Leuck-
Cyamus (Müller, '29, p. 58, Frey und Leuckart, '47, p. 205), *Gam-*
p. 57, Frey und Leuckart, '47, p. 205, Pagenstecher, '61, p. 31,
eydig, '78, p. 235. Grenacher, '79, p. 109); *Hyperia* (Gegenbaur,
er, '79, p. 111. Carrière, '85, p. 160); *Phronima* (Pagenstecher,
t, '78, p. 5, Claus, '79, p. 131); *Talitrus* (Grenacher, '79, p. 109);
dæ (Claus, '87, p. 15). I have observed an unfacetted corneal
rus, *Caprella*, and *Talorchestia longicornis*.

as smooth. The absence of facets from Amphipods is naturally
counted for by the absence of a definite arrangement among the ce
of the corneal hypodermis.

In the genus Tenais, the systematic position of which is probal
somewhere between the Amphipods and Isopods, the corneal cuticula
stated by Müller ('64, p. 2) to be facetted, at least in the males. A
cording to Blanc's ('83, p. 635) more recent observations, however, it
claimed to be unfacetted.

The *cones* in Amphipods have long been known to be segmente
The number of segments of which each cone is composed has been d
ferently stated, however, by different observers. According to Clap
rède ('60, p. 211), the cones in Hyperia are each composed of four se
ments. This also is the number given by Sars ('67, p. 61) and
Leydig ('79, p. 235) for Gammarus. Both Hyperia and Gammar
have since been carefully studied, and these observations are n
known to be inaccurate. Claparède was perhaps influenced in h
statement by his belief that all cones were composed of four cel
Sars was probably misled by the supposed fact that in Gammarus t
cone is surrounded by four bands of pigment, which sometimes give
the appearance of being divided into four segments.

The actual number of segments in the cone of Amphipods is tw
This number was first recorded by Pagenstecher ('61, p. 31) for t
cones of Phronima. Pagenstecher believed, however, that the con
in this Crustacean increased in numbers by division, and that th
showed no indication of being composed of two segments except wh
they were undergoing this process. I need scarcely add that subs
quent investigations have not confirmed Pagenstecher's belief. Con
composed of two segments have been observed in some six or sev
genera of Amphipods.[1]

The *retinula* in Amphipods is stated by different observers to cons
of either four or five cells. Five have been seen by Grenacher ('7
p. 653) and Carrière (85, p. 160) in Hyperia; by Grenacher ('7
p. 112), Claus ('79, Taf. VIII. Fig. 65), and Carrière ('85, p. 164)
Phronima; and by Mayer ('82, p. 122) in Caprella.

In Gammarus, Sars ('67, p. 61) observed that the cone had fo

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[1] In *Caprella* (Mayer, '82, p. 122), in *Gammarus* (Grenacher, '79, p. 110, C
rière, '85, p. 156), in *Hyperia* (Grenacher, 74, p. 652), in *Oxycephalus* (Claus, '
p. 151), in *Phronima* (Schmidt, '78, p. 5, Grenacher, '79, p. 112, Claus, '79, p. 13
in *Talorchestia* (Watase, '90, p. 296), and in the *Platyscelidæ* (Claus, '87, p. 1
In *Gammarus ornatus*, *Talorchestia longicornis*, and *Caprella*, each cone is compos
of two cells.

nds of pigment on it. Grenacher ('79, p. 110) took
ication that there were at least four retinular cells in
n of this genus, but he was unable to satisfy himself as to
were a greater number or not. Carrière ('85, pp. 156,
ntified the four cells first seen by Sars, and in favor-
ved what he thought might be indications of a fifth cell.
ornatus, as the present observations show, the retinula
ays composed of five cells, one of which, as Carrière
ally much smaller than the other four (compare *cl. rtn.'*,

tia, according to Watase ('90, p. 296), the retinula is
ly four cells. I have studied T. longicornis with the
rmining the number of retinular cells, and I find that,
are four large retinular cells, there is also one small one,
ore reduced than in Gammarus. Hence I conclude that
er of retinular cells in an ommatidium of Talorchestia

ment ('71, p. 151), that in Oxycephalus the retinula is
ed of four cells, is probably inaccurate, as Grenacher
ggests; and the same is perhaps true of Della Valle's
ervation, that in the Ampeliscidæ the retinulæ contain
each. It is therefore probable that the retinula in all
omposed of five cells, although possibly in some excep-
number may be four.

cells in Gammarus envelop the sides of the cone, as
ed, and extend distally as far as the corneal hypodermis
. In Hyperia and Phronima, according to the descrip-
s given by Carrière ('85, p. 161, and Fig. 128, p. 165),
ar to be limited to the proximal part of the retina.

e in Amphipods, first described by Pagenstecher ('61,
ylindrical element in the eye of Phronima, presents a
cture. In Hyperia, according to Grenacher ('77, p. 31),
d-like body, composed of five rhabdomeres, one for each
In Phronima, as Claus ('79, p. 128) has shown, the
ubular structure with five sides. Each side of the tube,
in the figure given by Carrière ('85, p. 165, Fig. 128),
a rhabdomere. In Gammarus locusta, Grenacher ('77,
own that, in transverse section, the distal end of the
oss-shaped. In G. pulex, according to Carrière ('85,
al end of the rhabdome in section shows four rays, the

proximal five. In Carrière's opinion, these rays indicate the five rh domeres. In Gammarus ornatus, the species which I have studied, rhabdome (Plate I. Fig. 6, *rhb.*) is cross-shaped in transverse sect throughout its length. Each rhabdomere has the form of an el gated plate, which is folded on its longest axis, so that its halves at right angles to each other. In the rhabdome, the four rhabdome lie so that their folded edges occupy the axis of the ommatidiu Each of the four large retinular cells rests in the furrow produ by the folding of a rhabdomere (compare Fig. 6). The fifth retinu cell always lies at the end of one arm of the cross-shaped rhabdo The two rhabdomeric constituents of that arm usually separate sligh so as to allow the small retinular cell to slip in between them. Po bly this cell produces a small rhabdomere, as the corresponding cell G. pulex does; but if such is the case, the rhabdomere must be a v small one, for I have not been able to discover it. A rhabdome essentially this structure occurs in Talorchestia.

As the preceding account shows, the rhabdome in Amphipods alw presents some indication of the number of rhabdomeres of which it composed. This number is usually five, although it is possible that Gammarus it may be only four.

In addition to the cells which have thus far been described as enter into the composition of the retina in Amphipods, certain other cells n be present. These may be embraced under the one head of *access pigment cells.*

In Gammarus, as Carrière ('85, p. 159) has shown, the space betw the ommatidia is filled with rather large cells, the nuclei of which usually visible with ease (Fig. 2, *nl. h'drm.*). These cells extend fr the basement membrane very nearly, if not quite, to the corneal hy dermis. In the fresh condition they contain a whitish opaque pigme On account of their having no definite arrangement, it is difficult to es mate their number, but there are probably two or three for each omn tidium. Cells similar in position to these have been described by Wat ('90, p. 296) in Talorchestia.

In Hyperia there are apparently three kinds of accessory pigme cells. One kind occurs in the region of the basement membrane (C rière, '85, p. 161, Fig. 124, *m.*); another kind surrounds the proximal p tion of the cones (Carrière, '85, p. 161); a third kind is applied to t retinulæ, and, according to Carrière, exactly equals in number the ce of the retinula itself. Possibly the cells which Grenacher ('79, p. 11 described as lying at the distal end of the retinula in Hyperia belo d, although, as must be remembered, Grenacher states only two such cells for each ommatidium.

inds of accessory pigment cells, with the possible excepich surround the retinula, occur in the lateral eyes of ère, '85, p. 164).

g is known about the source of the accessory pigment ods. Those in Gammarus have no resemblance to the c tissue which lies in the neighborhood of the eye, and y derived from the original ectodermic thickening which retina. Although some of the accessory pigment cells Phronima have been called connective-tissue cells (Claus, rière, '85, p. 160), a name which might be taken to imave come from a mesodermic source, nothing is really nem which would be inconsistent with an ectodermic

going account of the ommatidia in Amphipods the followbe made: cells of the corneal hypodermis not definitely bout nine to twelve, — possibly two to each ommatidium; retinular cells, five, — possibly in some cases four; accells (ectodermic ?) present. Of these last there may be s in Gammarus and Talorchestia, or there may be three eria.

Phyllopoda.

a in the eyes of Phyllopods present at least two strucof which obtains in the Branchiopodidæ and Apusidæ, Estheridæ and Cladocera. On account of the greater eyes in the Apusidæ and Branchiopodidæ will be conn the eyes in the Estheridæ, and finally those in the

æ and Apusidæ. — The ommatidia in these two families, the Branchiopodidæ, have been carefully studied by a petent investigators; their structure is consequently

which I used in studying these eyes consisted of specipus, probably B. vernalis, Verrill, which I had collected hood of Philadelphia, and which had been preserved n strong alcohol. Through the kindness of Dr. W. A. also able to examine a specimen of Apus lucasanus, A *corneal hypodermis* has been described by Claus ('86, pp. 321, in Branchipus and Apus. In Branchipus torticornis, according to C the nuclei of the hypodermal cells are arranged around the distal e each cone in circles of six; each nucleus participates in three circl that there are in reality only twice as many hypodermal cells as are ommatidia. The corneal hypodermis in the eye of Branchipu nalis (Plate IV. Fig. 30, *nl. h'drm.*) is similar to that described by in B. torticornis. According to Patten ('86, p. 645), a corneal hyp mis is present in Branchipus Grubii, but the cells, instead of regularly placed, as in either Branchipus torticornis or B. vernali stated to be indefinitely arranged.

The *corneal cuticula* in Apus is described as unfacetted by M ('29, p. 56), Burmeister ('35, p. 533), Zaddach ('41, p. 46), and und Leuckart ('47, p. 205). In Branchipus stagnalis the cutic smooth according to Spangenberg ('75, p. 30), marked by con convex facets according to Grenacher ('79, p. 114), and smooth nally but facetted internally according to Leydig ('51, p. 295). difference of opinion is probably due to the fact that in this specie facets are so poorly developed that their form can be determined with difficulty. In Branchipus vernalis, although the corneal cut is facetted, the facet is not thickened in its centre, but has the of a simple concavo-convex elevation, as described by Grenach B. stagnalis. In Branchipus paludosus according to Burmeister p. 531), in B. torticornis according to Claus ('86, p. 320), ar B. Grubii according to Patten ('86, p. 645), the corneal cutic unfacetted.

The *cone* in Branchipus, as Spangenberg ('75, p. 30) first de strated, is composed of four segments. This observation has since confirmed by Grenacher ('79, p. 115), Claus ('86, p. 320), and P ('86, p. 645). In Branchipus vernalis (Fig. 31, *con.*) the cone, acco to my observation, consists of four segments. The cellular natu each segment was first clearly stated by Grenacher. Each co Apus, according to both Grenacher ('79, p. 115) and Claus ('86, p. is composed of four cells.

The *retinula* in both Apus and Branchipus consists of five cells. number has been seen in both genera by Grenacher ('74, p. 653) a Claus ('86, p. 319). Spangenberg, however, ('75, p. 31) counted nuclei in the retinula of Branchipus. Since these unquestionabl resent the nuclei of the retinular cells, and since these cells are us five in number, Spangenberg's enumeration is probably inaccurate.

fluenced when counting the nuclei by his belief that the
as characteristic of many structures in the ommatidium.
vernalis (Plate IV. Fig. 32, *cl. rtn.'*) the retinula contains

e in Apus is short; in Branchipus (Fig. 30, *rhb.*) it is
In transverse section (Fig. 32, *rhb.*) it is circular, or at
but never pentagonal, as might be expected from the
surrounded by *five* retinular cells.

n B. vernalis contains no other cells than the three kinds
ed. According to Claus ('86, p. 319), blood corpuscles
way into the base of the retina of B. torticornis.

eceding account, the number of cells in the ommatidia of
didæ and Apusidæ can be stated as follows: cells of the
rmis, usually two, possibly variable in number in some
ells, four; retinular cells, five. In Branchipus torticornis
idial space may contain blood corpuscles.

The species which I studied as a representative of this
nnadia Agassizii, Packard. This species can usually be
eat abundance during summer in small fresh-water pools
orhood of Wood's Holl, Mass., where my material was
d for me by Mr. W. M. Woodworth.

surface of the retina in Limnadia, as I have mentioned
of the general structure of the eye in this genus, is cov-
extremely delicate corneal cuticula. This cuticula does
least trace of facets.

below the corneal cuticula are numbers of small nuclei
37, *nl. crn.*). These, from their position, are probably
as the nuclei of the corneal hypodermis. They are not
ged, and, although they sometimes lie between the cu-
distal end of a cone, they more frequently occur next
in the spaces between the cones.

ach *cone* in Limnadia is composed of *five* cells (Plate IV.
8). In this respect it resembles the cones in Estheria
E. tetracera described by Lenz ('77, p. 30). In Lim-
, however, cones composed of *four* cells are not infre-
ith (compare Figs. 37 and 38). Grube's ('65, p. 208)
t the cone in Estheria is composed of two segments is
eous, but Claus's ('72, p. 360) statement that in Limnadia
sts of four segments may be accurate, contrary to the
z.

The *retinular cells* in Limnadia cover the greater part of the sides of the cones, and completely hide the rhabdome (Plate IV. Fig. 36). Their number can be determined in transverse sections in the region of the rhabdome. In such sections each rhabdome is surrounded by five retinular cells (Fig. 39, *cl. rtn.'*). Occasionally nuclei can be distinguished in the pigment about the base of the cone. These are probably the nuclei of the retinular cells.

Besides the elements thus far enumerated, the retina in the Estheridæ is not known to contain other kinds of cells. The cells in the ommatidia of this family are, therefore, as follows: cells of the corneal hypodermis, not regularly arranged; cone cells, usually five, sometimes four; retinular cells, five.

Cladocera. — The extreme minuteness of the ommatidia in the eyes of the Cladocera renders their study especially difficult. In an undetermined species of Evadne which I have studied, the ommatidia are comparatively large, and in this respect are especially favorable for investigation. In the particular specimens which I used, however, I was entirely unsuccessful in all attempts to differentiate the nuclei. Although I tried a number of dyes and reagents, I was never able to make these structures visible. In consequence of this, there are several important questions concerning the eyes in the Cladocera which I have not been able to answer.

It is reasonable to believe that a corneal hypodermis much like that in Limnadia is present in Evadne, but, probably on account of my inability to stain the nuclei, I have seen no traces of it.

The *cones* in Evadne are very clearly composed of five segments (Plate IV. Figs. 41, 42). At their distal ends the cone cells are expanded so that their peripheral membranes (Fig. 41, *mb. pi'ph.*) are in contact with one another. At this level, however, the substance of the cone proper is collected about the axis of the ommatidium. Proximally the peripheral membranes of each cone contract, and under these circumstances the cavity of each cone cell is apparently filled completely with the differentiated material of the cone itself (Fig. 42).

A cone composed of five segments has been observed in a considerable number of Cladocera. Thus it is known to occur in Bythotrephys (Leydig, '60, p. 245, Claus, '77, p. 144), Daphnia (Spangenberg, '76, p. 522, Grenacher, '79, p. 117), Polyphemus, Evadne (Claus, '77, p. 144), Podon (Grenacher, '79, p. 117), and Leptodora (Carrière, '84, p. 678). Weismann's assertion ('74, p. 364) that the cone in Leptodora is composed of four segments is disproved by Carrière's later observations, and

nt ('76, p. 372) that the same number of segments oc-
ne of Sida is probably erroneous. There is, therefore,
e that the cones in the Cladocera are always composed
s.

ion of the *retinula* in Cladocera, so far as I am aware, has
worked out. In Evadne, on account of the relatively
ommatidia, the number of cells in the retinula can be
t the proximal end of the cone, this structure is sur-
r distinct masses (Fig. 43). The regularity with which
cur leaves no doubt as to their number. Each one prob-
a retinular cell. In transverse sections made through
Plate IV. Fig. 45), this structure is surrounded by *five*
of which I take to be a retinular cell. It is therefore
he retinula of Evadne is composed of five cells, four of
nearer the surface of the eye than the fifth.

have seen no evidence of the existence of other cells than
to the cone and retinula. According to Carrière ('84,
terommatidial space in Leptodora contains a number of
lop the cones more or less completely. These are proba-
ed as accessory pigment cells.

regoing account the following general statement can be
mmatidia in the Cladocera: corneal hypodermis, not
cells, five; retinular cells, five (in Evadne); accessory
resent (in Leptodora).

Copepoda.

d the lateral eyes in Pontella and Argulus, as representa-
epods. As is well known, the eyes in these two genera
structure, and I shall therefore describe them separately,
the eyes in Pontella.

—The species of Pontella which I studied was extremely
wport in August, 1890. This animal was so transparent
t the general structure of its eyes could be ascertained
roscopic inspection of it. In addition to its median eye,
a ventral position, it possesses a pair of lateral eyes
, '63, Taf. III. Fig. 5) situated one on either side of the
the antero-dorsal angle of the head.

eye in Pontella, as Claus ('63, p. 47) has already stated,
a spherical lens (Plate II. Fig. 18, *lns.*), which is usu-
ched to the superficial cuticula. Immediately behind

this lens, and in fact covering much of its proximal face, is a rather irregular mass of cells, the retina. In the living animal the cells of the retina contain a great quantity of black or reddish black pigment. This coloring matter, however, is so readily soluble in alcohol, that in specimens preserved in that fluid all traces of it disappear. The optic nerve (*n. opt.*, Fig. 18), an imperfectly defined bundle of fibres, emerges from the retina near its posterior dorsal edge, and passes directly backward to the brain.

The lenses of the two lateral eyes in Pontella are so near each other that their median faces are almost in contact (compare Plate III. Fig. 29). The retinas of the two eyes, as Claus ('63, p. 47) has observed, are united with one another on their median faces, and so intimately that they are apparently incapable of independent motion.

The two retinas together may be rotated on their lenses through an angle of about forty-five degrees. The plane of this rotation corresponds to the sagittal plane of the body, and the rotation is accomplished by two pairs of muscles, one for each retina (compare Claus, '63, Taf. III. Fig. 6). One pair of these muscles is shown in Figure 18. They occupy a plane approximately parallel to the sagittal plane of the body, and the effects of their contractions must be apparent from their positions. When both muscles are relaxed, the retina occupies a position substantially as shown in Figure 18. By the contraction of the posterior muscle, the retina may be drawn upward and backward over the surface of the lens, till its axis, instead of pointing dorsally, is directed forward and upward at an angle of about forty-five degrees with its original position. The retina is not usually held for any great length of time in this position, but is soon returned by the contraction of the anterior muscle to its normal place. The backward motion of the retina is accomplished with such rapidity that the animal has the appearance of winking. The forward motion is rather slower.

Each lens in Pontella is composed of concentric laminæ (Plate III. Fig. 29, *lns.*). A considerable portion of its distal surface is intimately connected with the superficial cuticula (Plate II. Fig. 18), although a line of demarcation between lens and cuticula can always be distinguished.

When the anterior half of the body of Pontella is boiled in a strong aqueous solution of potassic hydrate, and afterwards subjected to the action of concentrated nitric acid, all the soft parts are dissolved, and only the very resistant chitinous structures remain. In specimens treated in this way, the lenses retain their firm connection with the superficial cuticula, and differ in appearance from those in the living ani-

t their concentric lamellæ are somewhat more distinct.
ne lens is composed of concentric layers indicates that
d the resistance which it offers to reagents is weighty
r of its chitinous nature. In my opinion, therefore, the
is a chitinous secretion.

ent of the lens in Pontella is rather peculiar. Appar-
is formed with each moulting of the general cuticula;
her large proportion of the number of individuals exam-
were abnormally small, having a diameter of one third
th of that shown in Figure 18. Moreover, in all such in-
perficial cuticula was correspondingly thin and delicate,
nimal was subjected to boiling potash, the segments of
pendages separated with a readiness never observed in
large lenses. There can be no doubt, I believe, that the
always accompanied by thin cuticula, a relation which
d by the immature condition of both structures.

lenses differ from the larger ones in only one important
es that of size. They are not in contact with the super-
This relation can be determined better in optical sec-
ctual ones, for in the latter the position of the lens is
at changed by the resistance which it offers to the knife.
he small lens occupies a position relatively the same as
e lens, the space between the surface of the small lens
l cuticula being filled with a cellular mass. This mass,
cal sections, apparently envelops the lens on all sides,
dly composed of the cells which secrete that structure.
eases in size, the cells are probably excluded from the
it and the cuticula, and as they retreat cement the lens
Upon the completion of the lens, the cells which have
cing it probably withdraw slightly from it to form the
ckenings which occur beneath the adjoining cuticula
18, and Plate III. Fig. 29, *h'drm.*). These thickenings
ei, and often have delicate strands of protoplasm stretch-
ce of the lens (Fig. 18).

t these facts justify the opinion that the lenses in the
Pontella are composed of chitin, that they are produced
h the superficial cuticula, and that they are secondarily
Like the cuticula itself, they are products of the hy-
lens being generated in all probability with each new
ticula.

Lenses similar in position to those in Pontella have been identif in the lateral eyes of several other genera of Copepods. Gegenba ('58, p. 71) described such lenses in Sapphirina, and Leuckart (' p. 250) observed similar ones in the lateral eyes of Corycæus a Copilia. In all these genera the lenses, although biconvex, are n spherical, as in Pontella. Gegenbaur ('58, p. 71), following Leydi generalization, believed that in Sapphirina the lenses were thickeni in the cuticular covering of the body, and Claus ('59, p. 271) conside them morphologically equivalent to a single corneal facet. Leuck ('59, p. 250), without definitely committing himself as to the nat of the lens, states that in Copilia and Corycæus the lens is implan in the superficial cuticula, and further describes it in Corycæus as co posed of two parts, an outer and an inner. According to Grenac ('79, p. 67), both parts can be identified in the lens of Copilia; outer part is a portion of the superficial cuticula; the inner part, b in its optical properties and its behavior toward reagents, is unlike cuticula. The inner part, however, contains no traces of cells, but composed of a homogeneous substance, probably secreted. This view the duplicity of the lens contrasts with the older idea of its origin a thickening in the superficial cuticula.

It is possible that the lenses in the Pontellidæ and Corycæidæ are homologous structures, but on account of their similarity I am incli to consider them as such. Since in Pontella both parts are deri from the cuticula, I believe that a similar origin will be demonstra for these parts in the Corycæidæ. The differences which Grenac has pointed out between the two parts of the lens in Copilia do necessarily oppose this view. It is possible that the cuticular secret which forms the proximal part of the lens may originate separat from the other cuticula, as in fact it does in Pontella; and it may a be true, although this is not supported by the condition in Ponte that the two parts, although both secretions of the hypodermis, m differ enough in their substance to account for all the peculiarities served by Grenacher.

The *retina* and lens in Pontella are not separated by an interven space as in the Corycæidæ, but are in immediate contact. The ret is composed of a mass of cells, the number and arrangement of wh can be seen in the figures on Plate III. These figures represen series of consecutive sections cut in planes transverse to the axis the eye, i. e. parallel to the horizontal plane of the animal (comp Fig. 18, Plate II.). The series is complete in that it represents

ich pass through the retina. The most ventral section
ure 20, the most dorsal in Figure 29.

below the lens the central part of the retina is occupied
granular mass (Fig. 18, *con.*), which in the living animal
without pigment. In transverse sections this mass is
of two bodies (*cl. con. 1*, and *cl. con. 2*, Fig. 25), which
s to the lens (compare Figs. 25–27). Each body con-
(*nl. con.*, Figs. 25 and 27) and consequently represents
he position which the mass occupies, and from the fact
no pigment, it represents, I believe, a cone, and the two
t is composed are its two segments.

47) states that in Pontella each retina is provided with
all crystalline cones, but my own observations do not
tement. The body which, on account of its position, I
as the cone in Pontella, is probably homologous with
p. 133) first described as the inner lens in Corycæus,
ubsequent investigators have called the crystalline cones
Gegenbaur, '58, p. 71) and Copilia (Leuckart, '59, p. 252).
ve, is known of the cellular composition of the cone in

ent of the elements in that portion of the retina which
one in Pontella is not easily made out. The most con-
ures in this region are rod-like bodies, which probably
omeres. Eight of these, arranged in three groups, are
retina. The largest group, composed of five rods, lies
the cone. The rods of this group have been numbered
ve in the retina to the left in Figures 21, 22, and 23.
s group, in the same retina, is the sixth rod, seen in
and 26. Anterior to it are the seventh and eighth
gures 26, 27, 28, and 29.

of the cells to which these rods belong cannot always be
that there is a cell for each rod is evident from the fact
od there is a large nucleus. The nucleus belonging to
ich the eighth rod was produced is shown in Figure 28
belonging to the cells from which the sixth and seventh
dicated in Figure 26 (*nl. rtn'.*), and those belonging to
hich the central group of five rods came are seen, four in
ne in Figure 25 (*nl. rtn.'*).

o these nuclei, which judging from their positions and
questionably the nuclei of the cells to which the rhab-

domeres belong, the retina contains a number of smaller nuclei (Fig. 21, *nl. h'drm.*). These nuclei have been drawn in the figures of the various sections in which they occur, and probably represent undifferentiated cells.

To what extent the retina of Pontella can be resolved into ommatidia may be seen from the foregoing account. Evidently the two cone cells, the subjacent groups, of five retinular cells, and probably some of the undifferentiated cells, are the equivalent of one ommatidium. The sixth cell, with its rod, is probably the representative of a second ommatidium, and the seventh and eighth cells are probably representatives of one, or perhaps two, more.

If this interpretation be correct, the cells in the one complete ommatidium in Pontella would be as follows: corneal hypodermis, undifferentiated; cone cells, two; retinular cells, five; undifferentiated pigment cells (ectodermic?) present.

Each retina in Sapphirina, according to Grenacher ('79, pp. 69, 70), contains one group of three rhabdomeres. These are accompanied, as in Pontella, by an equal number of large nuclei. The body designated at *y*, and perhaps some of those marked *x*, in Grenacher's figure of Sapphirina (Fig. 43), may also represent isolated rhabdomeres. In Copilia, Grenacher believes that the number of rhabdomeres in each retina is three. Possibly in this genus, as in Sapphirina, the body marked *x* by Grenacher (Taf. VI. Fig. 40) may represent an isolated rhabdomere. Grenacher's observations, when coupled with what I have seen in Pontella, show that in Copepods the number of retinal elements is open to considerable variation, and that what would correspond to the retinula in Sapphirina, and perhaps in Copilia, consists of a cluster of only three cells, instead of five, as in Pontella.

Branchiura. — The ommatidia in Argulus are rather small, and their structure is consequently imperfectly known. The specimens of this Crustacean which I studied were obtained from an aquarium in which the common Killifish, Fundulus heteroclitus, had been kept. I have not been able to determine the species to which these specimens belong.

The *corneal hypodermis* in Argulus is separated from the retina proper by a space filled with blood (Plate II. Figs. 11, 12, *cœl.*). The cells in this layer (Fig. 12, *h'drm.*), as in the corneal hypodermis of Amphipods, are not arranged in groups, but are irregularly scattered. On their distal faces they produce the corneal cuticula (Fig. 12, *cta.*), which, as Müller ('31, p. 97) observed, is without facets. Proximally they are separated from the blood space by the delicate corneal membrane (Fig. 12, *mb. crn.*).

ce of the retina proper in Argulus is bounded by a deli-
nembrane (Figs. 11–13, *mb. pr'con.*) and its proximal face
e basement membrane (Figs. 11–13, *mb. ba.*).

nspicuous objects in the retina are the *cones* (Fig. 11,
e with their distal ends usually somewhat below the
rane (Fig. 13). Each cone, as Claus ('75, p. 256) has
nposed of four segments (Fig. 14). The segments corre-
and although the cone itself terminates proximally before
habdome, the cone cells form an axis free from pigment
from the cone to the rhabdome (compare Fig. 12). In
ections the peripheral membranes of the cone cells (Fig.
can be distinguished as sharply marked lines which ex-
sides of the cone to the sides of the rhabdome. The
embranes of the cone cells in the region between the cone
are apparently marked by thickenings which appear in
nal and transverse sections (compare Figs. 13 and 15).
nd of the rhabdome the four cone cells separate, and, after
around the rhabdome, become lost in the adjoining tissue
n.). I have not been able to discover the nuclei of the

t to determine the number of cells in the *retinula* of Argu-
below the proximal end of the rhabdome, the retinula is
ve distinct pigmented masses (Fig. 17, *cl. rtn.'*). Since the
g. 16, *rhb.*) is composed of five rhabdomeres, it is highly
the retinula consists of five cells; but I have not been able
vith precision the outline and extent of these cells.

which are visible in the retina of Argulus closely resemble
They are limited for the most part to two regions (Fig.
the level of the cones, the other near the basement mem-
rently there are no nuclei immediately below the preconal
Those which are near the cones (Figs. 13, 14, *nl. h'drm.*),
their arrangement and position, probably represent inter-
igment cells. Those near the basement membrane (Fig.
may be the retinular nuclei, as their position seems to indi-
me distance proximal to the basement membrane, nuclei
'drm.') occur among the nerve fibres. Possibly they repre-
d cells in this region, but the strong resemblance which
the nuclei on the distal side of the membrane induces me
at they too are retinular nuclei, which, as in the Amphi-
igrated to a position below the basement membrane.

The cells in the ommatidium of Argulus are as follows: cells of the corneal hypodermis, not arranged in definite groups; cone cells, four; retinular cells, probably five; accessory pigment cells probably present.

Isopoda.

The material which I used in studying the eyes in Isopods came from several sources. I collected specimens of Asellus and Porcellio in the neighborhood of Cambridge, and the two species of Idotea which I studied were obtained at Newport. Specimens of Serolis Schythei, Lütken, and of an undetermined species of Sphæroma, were kindly furnished me from the collections in the Museum.

The ommatidia in Isopods present two types of structure: one of these is characteristic of the eyes in a majority of the members of this group; the other, so far as is known, is represented only in the genus Serolis. These two types will be considered separately, and the one which is common to the greater number of Isopods will be described first.

The *corneal hypodermis* in the more common of these two ommatidial types was first identified by Grenacher. In Porcellio, according to this author ('79, p. 107), the proximal surface of each facet is covered with two comparatively thin cells. These are the cells of the corneal hypodermis. Bellonci ('81^a, p. 98, Tav. II. Fig. 11 n.) figures similar cells in the ommatidium of Sphæroma, and Beddard ('90, p. 368) concludes justly, I believe, that, of the four nuclei found near the distal end of the cone in Arcturus, two represent cone cells and two cells in the corneal hypodermis. In Idotea irrorata I have identified two cells in the corneal hypodermis for each ommatidium. The nuclei of these cells lie very near the nuclei of the cone cells (compare *nl. con.* and *nl. crn.* in Figs. 50 and 51, Plate V.). In an ommatidium of Porcellio, Grenacher ('79, pp. 107, 108) observed that the plane which separates the two cone cells also separates the two cells in the corneal hpyodermis. In Idotea, also, both kinds of cells are separated by a single plane.

The facetted condition of the *corneal cuticula* of Isopods was observed as early as 1816 by G. R. Treviranus ('16, p. 64), in wood-lice, and subsequently in the same animals by Lereboullet ('43, p. 107, '53, p. 119). The shape of the facets in different Isopods has given rise to some difference of opinion. According to Müller ('29, p. 42), in Cymothoa each has the form of a biconvex lens. Leydig ('64^a, p. 40) states, however, that in Oniscus the facets are concavo-convex with their hollow faces innermost. In Asellus, according to the figure given by Sars ('67, Planche VIII. Fig. 14), they are plano-convex with their flat faces ese differences, although at first sight somewhat con- ot matters of great importance, for it is probable that opod sheds its cuticula and a new one is formed, the successive stages of its growth, outlines which coincide h those recorded by the different observers. Thus, an d be represented by the concavo-convex lens described ntermediate stage by the plano-convex lens figured by al condition by the biconvex lens mentioned by Müller. he explanation of the differences, or the observations of s are probably erroneous, for the results of the more ions point to the conclusion that the facets in Isopods of a biconvex lens. Facets of this shape have been seen 77, p. 29) in Porcellio, and by Bellonci ('81^{a}, p. 98) in cording to my own observations, they also occur in Porcellio, and, as I shall show subsequently, in Serolis. ra mentioned the inner face of each facet is distinctly lso true of the outer face in Asellus and Porcellio. In tea (Plate V. Fig. 50), however, the outer face is so hat it is difficult to decide whether its curvature is that rneal cuticula or one peculiar to the facet itself.

in Isopods is composed of two segments was first ob- g ('64^{a}, p. 41, and '64, Taf. VI. Fig. 8) in Oniscus. Ac- author, each segment is spherical. Each ommatidium, ns two spheres, and these, as Leydig's figure shows, are de immediately below the corneal facet.

l known that in many Isopods, especially in the wood- elf is nearly spherical, and its two segments would con- nispheres, not spheres as figured by Leydig. How Ley- of the spherical shape of the segments can be accounted rent. Since the two spheres described by him occupy e positions as the hemispherical segments of a normal ot much question in my mind that they represent these ibly their separation and spherical form may have been ng action of some reagent which Leydig may have used ne transparent. A cone composed of two segments has y Sars ('67, p. 110) in Asellus, by Leydig ('78, p. 256) Grenacher ('77, p. 29) in Porcellio, by Bellonci ('81^{a}, roma, by Sye ('87, p. 23) in Jæra, and by Beddard Arcturus. In the three genera which I have examined, and Sphæroma, each cone consists of two segments.

These observations naturally lead to the conclusion that in all Isopods each cone is composed of two segments. To this general statement, however, there are two noteworthy exceptions, one recorded by Sars, the other by Beddard. Sars ('67, p. 110) has shown that, of the four ommatidia in each eye of Asellus aquaticus, three have cones composed each of two segments; in the fourth, however, the cone is divided into three parts. This observation has been confirmed by Carrière ('85, p. 155). It is important to observe that in the figure given by Sars ('67, Planche VIII. Fig. 12) the three parts of the cone are not of equal size; one is about as large as a single segment in the cones of the other three ommatidia, whereas the remaining two are each about half as large. In the eyes of the species of Asellus found about Cambridge, the ommatidia are usually twice as numerous as in the European species, A. aquaticus, and, so far as I could observe, the cones in the American species were always composed of only two segments. In Arcturus, according to the figures given by Beddard ('90, Plate XXXI. Figs. 1 and 4), cones of three segments are occasionally met with.

The cellular composition of the *retinula* in Isopods was first made out by Grenacher ('74, p. 653), who found that in Porcellio this structure consisted of seven cells. Distally these cells surround the cone; proximally they are continuous with the optic-nerve fibres. A retinula consisting of seven cells has also been demonstrated by Buller ('79, p. 513) in Cymothoa, and by Beddard ('88, p. 443) in Ægea and Ligia. As Beddard ('88, Plate XXX. Fig. 13) has shown, the seven cells in the retinula of Ægea pass through the basement membrane and become continuous with the nerve fibres. In Porcellio, as I have observed, the fibrous ends of the seven retinular cells not only can be identified as nerve fibres below the basement membrane, but each cell contains a well developed fibrillar axis (Plate V. Fig. 46, *ax. n.*), and I therefore conclude that in Porcellio all seven cells are functional as nervous elements.

In Idotea robusta, transverse sections of the retinula in the region where the rhabdome is thickest present the outlines of what seem to be *seven* retinular cells (Plate V. Fig. 48). In positions either distal or proximal to this, however, only *six* cells appear. These six cells pass through the basement membrane and taper into nerve fibres, and their nuclei, unlike the corresponding nuclei in other Isopods, occur in that part of the cell which is proximal to the basement membrane (Figs. 49 and 50, *nl. rtn'.*). The seventh body (Fig. 48, *cl. rud.*), in those sections in which it occurs, has in all essential respects the same appearance as any one of the adjoining six cells. It differs from these, however, in that mewhat smaller, and I therefore conclude that it is a l. It does not appear to contain a nucleus; granting, is a rudimentary retinular cell, one would look for its the region about the rhabdome, but in the region of ie other retinular cells, i. e. proximal to the basement ing to the irregularity with which the fibrous ends of lls are arranged in this region, I have not been able nucleus with this rudimentary cell. Neither have I us projections reaching from the rudiment of the cell ement membrane such as might be expected provided l a part of the rudimentary cell persisted below the vertheless, I believe, for the reasons already stated, a in Idotea robusta is composed of seven cells, one of ely rudimentary.

rata (Plate V. Figs. 53, 55) the retinula consists of only ich possess fibrillar axes, and are therefore probably funcs structures. In one retina of the several pairs of eyes d, there was a single ommatidium with *seven* functional With this one exception, however, I have not been able to the seventh cell in Idotea irrorata. In Arcturus, accord- '90, p. 368), the retinula is also composed of six cells.

, Bellonci ('81, p. 98, Tav. II. Fig. 12) has figured and nula consisting of *five* cells. These cells alternate with hich probably represent accessory pigment cells. If Bel- is correct, it must be admitted that the number of cells f Isopods may be as few as five. My own observations, confirm Bellonci's account. In the species of Sphæroma died, there are *seven* cells in the retinula, four of which ee small (Plate V. Fig. 58). All these cells pass through embrane; all the large ones, and certainly some of the lso connected with nerve fibres.

tions indicate that in the Isopods the retinula is comix or seven cells. If Bellonci's statements prove to be cture may be composed in some cases of only five cells, rvations are opposed to this view.

in Isopods presents two types of structure, one of well described by Grenacher ('77, p. 30) for Porcellio species the rhabdome is composed of seven rhabdomeres, mains in connection with the retinular cell which proansverse section the rhabdome has the form of a seven-pointed star, a ray corresponding to a rhabdomere. Each ray projects into its retinular cell, not between two cells. My own observations on Porcellio confirm Grenacher's statements. A second representative of this type of rhabdome has been described by Bellonci ('81, p. 98) for Sphæroma. Here, however, the rays, although they agree in number with the retinular cells, project *between* the cells, not into them.

The second type of rhabdome is well represented in the eye of Arcturus furcatus. In this species, according to Beddard ('90, pp. 368, 369), the distal portion of the rhabdome, although surrounded by *six* retinular cells, is bounded by *four* perpendicular sides. Each of the six cells appears from its position to contribute to the formation of the rhabdome, and yet in the greater part of this structure segments corresponding to rhabdomeres are not visible. In its proximal portion, however, the rhabdome, according to Beddard, is divided into six rhabdomeres, each of which is applied to its proper retinular cell. In Idotea robusta the rhabdome (Plate V. Fig. 48, *rhb.*) is nearly square in transverse section. So far as I have been able to discover, it does not show at its proximal end any indication of rhabdomeres.

Of these two types of rhabdome, the one in which the rhabdomeres are evident is probably more primitive than the one in which their individuality is almost, if not completely lost.

The retinas of Isopods may contain, in addition to those already mentioned, two other kinds of cells. Of these the one most frequently met with fills the space between ommatidia. Cells of this kind have been identified in Porcellio by Grenacher ('79, p. 107), and it is probable that the pigment cells described by Bellonci ('81, p. 99) as intervening between the retinular cells in Sphæroma belong to this class. I have observed interommatidial cells in Idotea; here they contain few or no pigment granules, but are easily recognized by means of their nuclei (Plate V. Fig. 54, *nl. h'drm.*).

The source of these cells is not definitely known, but there appears to be no evidence in favor of their having been derived from outside the retina. Grenacher believed that those in Porcellio are undifferentiated hypodermal cells; this interpretation probably holds good for those in Sphæroma and Idotea.

The hyaline cells, the second kind of accessory cells, have been identified by Beddard ('87, p. 235, '88, Pl. XXX. Fig. 9, *h.*) in Æga and Cirolana. Since these cells are best developed in the eyes of Serolis, a full description of their structure will be deferred until the account of the eyes in that genus is given.

characterize the ommatidia in Isopods (except Serolis) ells of the corneal hypodermis, two; cone cells, two; en, six, or possibly five. Undifferentiated hypodermal es present, and hyaline cells occur in a few genera.

peculiarities of the *ommatidia in Serolis* were first ded ('84, pp. 339–341) about seven years ago. Recently tions have for the most part been confirmed by Watase now be admitted without question that the ommatidia several important respects from those of many other

hich I used in studying the eyes in this Crustacean anced embryos and matured individuals of Serolis n. This material was collected in Patagonia by the n, and was preserved in strong alcohol. Fortunately, histological condition, and sections prepared from it rly the finer structure of the eyes. My observations, ccount will show, differ in no very important respects dard and Watase.

en's generalization, that a *corneal hypodermis* was to be pound eyes of all Crustaceans, led Beddard ('88, p. 447) Serolis, he was not able to identify it. Watase ('90, was more fortunate, and succeeded in finding under ells in the corneal hypodermis. I have not been as tase was in determining the exact number of hypoommatidium, but I have seen enough to convince me e present. In sections approximately tangential to the the adult retina, one occasionally finds nuclei (Plate *n.*) between the distal ends of the cone cells and the These represent unquestionably the cells of the corand are not to be confused with the nuclei of the cone n a deeper plane. In making sections, the corneal d so irregularly that the tissue immediately below it isarranged. It was therefore possible to get only irof the tissue in this region, such as Figure 60 shows, ents were always too small to admit of an accurate the number of hypodermal cells under a single facet. equally unsuccessful in my attempts either to isolate tudy them *in situ* on the corneal cuticula.

he adult, owing to the thickness of the cuticula, are e study of the corneal hypodermis; but in embryos of even an advanced stage, the cuticula is so thin that the hypodermis can be studied with comparative ease. An ommatidium from the eye of an advanced embryo is seen in Figure 65; the ommatidium is viewed from the side. Distal to the cone (*con.*) four nuclei can be seen; one (*nl. crn. 1*) is superficial in position, three are deep. The relation of these nuclei to the ommatidium can be satisfactorily studied in sections transverse to the axis of the ommatidium. A series of three such sections is seen in Figures 66, 67, and 68. Of these, the most distal is that shown in Figure 66. This includes only the most superficial layer of the retina, and contains two nuclei (compare *nl. crn. 1*, in Figs. 65 and 66). These nuclei, as their position clearly indicates, represent cells of the corneal hypodermis. In the plane of the section which includes the three deeper nuclei of Figure 65, four nuclei are in reality present (Fig. 67); two of these (*nl. con.*) are large, and lie directly below the superficial ones in the corneal hypodermis; two are small (*nl. crn. 2*) and lie between the ends of the deeper large nuclei. Of the deep nuclei, the two large ones (*nl. con.*) rest one above each segment of the cone; in fact, as a section in a slightly deeper plane shows (Fig. 68, *nl. con.*), these nuclei coincide so closely with the segments of the cone that they must be regarded as the nuclei of the cone cells.

It is difficult to state what nuclei in the adult correspond to the smaller of the four deep ones in the embryo. The number of these nuclei (two) in the embryo equals the number of pigment cells which Watase ('90, p. 294) has described as surrounding the cone; but that these nuclei do not belong to such cells is evident from the fact that in the embryo, the nuclei of the pigment cells can be identified in a position somewhat proximal to that in which the smaller of the four nuclei occur (compare *nl. dst.* in Figs. 65 and 69.) Possibly the cells represented by these small nuclei in the embryo become in the adult the small interommatidial pigment cells, or it may be that they retain their relatively superficial positions, and, while occupying the space between the corneal facets, perhaps produce the cuticula of that region. In the fragments of the adult retina, from immediately below the corneal cuticula, small nuclei are not unfrequently met with in the spaces between the ommatidia. These are possibly derived from the smaller deep nuclei of the embryo.

It will thus be seen that my conclusions concerning the corneal hypodermis agree in the main with those of Watase; namely, that for each ommatidium there are two cells in this layer. Besides these, however, it is possible that the hypodermis may contain an equal number of other upy positions immediately under the cuticula and be-atidia.

the *corneal cuticula* of Serolis, when viewed from the gularly circular in outline, often approaching a six-sided e already observed, they are arranged on the plan of the The distal face of each facet is flat, or only slightly ximal face is decidedly convex. The curvatures of the e thickness of the cuticula in the facet of S. Schythei me as that figured by Watase ('90, Plate XXIX. Fig. 1) hich he studied.

Beddard ('84, p. 340) first demonstrated, and as Watase terwards confirmed, is composed of two nearly hemi-its, which correspond to the two cone cells. The proto-of each cone cell covers the curved surface of the seg-t belongs, and contains a nucleus in its distal portion. have been well shown by Watase ('90, Plate XXIX.

dition presented even in advanced embryos (Fig. 65) the part of the cone earliest formed, is the one which plied faces of the two cone cells, and that from this as has continued to increase outwards. Although at this of the cone itself is sharply marked (Fig. 65), the ex-the cone cells are only approximately indicated by the he pigment granules, which have begun to form in the ment cells.

in Porcellio and Idotea, the cone cells and the cells of dermis are separated by the same perpendicular plane. complications in the structure of the cone cells which subsequently with greater clearness.

in Serolis, as Beddard ('84, p. 340) first observed, is it is composed of only *four* cells. My own observations ing that is new to the previous accounts of this structure. h Watase has drawn ('90, Plate XXIX. Fig. 1) of the m of the retinular cell when viewed from the side and ts rhabdomere, reproduces very closely the structural I have observed in S. Schythei.

in Serolis has been carefully studied by Beddard ('88, Owing to the complexity of its structure, one meets with empting to interpret its parts in terms of the relatively of many Crustaceans. The peculiarities of this structure can be approached most satisfactorily perhaps from the side o adult anatomy.

In a transverse section of the distal end of the rhabdome, five st tures can be observed (Fig. 61). Four of these (Fig. 61, *rhb'm.*) squarish pieces confluent on one side with a retinular cell, and in con with one another only at their angles The sides of these pieces wl are directed towards the axis of the ommatidium are convex, and gether bound a central area which contains the fifth or axial struc (*cl. con.*). Each of the squarish pieces also exhibits a line slightly conc towards the axis of the ommatidium. This line, which might be ta for the separation between the axial and peripheral structures, is in r ity entirely within the latter. That these are five separate structu is indicated by the fact, that in transverse section, when for any rea the elements have been broken apart, the separation almost always oc on the lines which I have described as the limits of the different piec

Evidently the squarish masses (*rhb'm.*) on the axial faces of the ret lar cell correspond to the rhabdomeres of other Crustaceans, and like tl structures are produced by the cells to which they are attached. I more difficult to explain the axial element, for it shows no indicatio having been produced by the surrounding retinular cells, nor are tl other cells in the neighborhood to which its production could referred.

When the longitudinal extent of these structures is considered, difficulty of explaining the axial portion is increased. In S. Schy the rhabdomeres extend only a short distance distally and proxima but throughout the whole of that distance they are closely applied the axial face of the retinular cells. This condition has been well figu by Watase ('90, Plate XXIX. Fig. 1), and supports the statem already made that these bodies correspond to the rhabdomeres in ot Crustaceans. I have never observed a rhabdomere, such as that figu by Beddard ('87, p. 234), in which the proximal half of the struct is not in contact with the retinular cell. The axial part has a m more considerable extent in a longitudinal direction than the rl domeres. Apparently it is continued proximally into a fibrous bun which stretches towards the basement membrane, where according Beddard ('88, p. 449) it may terminate as a single fibre.

From what has just been stated it must be evident that the so ca rhabdome of Serolis consists of two sets of structures, one of wl includes the four rhabdomeres and the other the axial part with its p imal fibrous prolongation.

ment of these structures has been studied by Beddard In the youngest embryos which he examined, the axial eady formed, and at that stage it was closely invested by ar cells and two other cells, the hyaline cells. Judging ions, Beddard believes that both kinds of cells may con- formation of the axial structure, although the fact that arish in transverse section leads him to conclude that the ells play the more important part in its formation. Bed- e axial body as the rhabdome of the immature eye. In his bdome in the adult is produced by subsequent secretions lar cells, and presents the form of the four rhabdomeres ed. Although these rhabdomeres form the principal part e in the adult eye, he believes that the rhabdome of the ersists as the axial fibrous structure in the later stages, perhaps the greater part of its distal continuation abdomeres.

such explanation of the origin of the axial part of the at proposed by Beddard be accepted, it is difficult to the fibrous portion could arise as a secretion; for in the imal portion of it is touched by neither retinular nor

the moment the adequacy of Beddard's explanation of e axial part, we are still confronted by what appears to alleled in the structure of the eyes in Arthropods, namely, which produces two distinct rhabdomes. This may not lity, but if it occurs at all, it is certainly exceptional.

wever, that the so called axial part of the rhabdome in le of another interpretation, against which the objections ed cannot be urged. That the axial portion terminates he basement membrane has been fairly well established The distal termination of it, however, has not been so it. It is my belief that the axial structure is directly lly with the cone cells; in other words, that this struc- garded as a proximal extension of the cone cells, not as rhabdome. The termination at the basement mem- rolongation of the cone cells, as observed by Beddard, sistent with the interpretation which I have suggested, condition in Serolis similar to that in Homarus, where of the cone cells also terminate on the basement mem- he fibrous structure should be present in the embryo of

Serolis before the formation of the rhabdome proper is rather in f of my interpretation than opposed to it. The direct evidence that axial body is a proximal extension of the cone cells is not as conclu as could be desired. The condition which most favors this view i follows. In longitudinal and transverse sections of the ommatidia, l in adult and embryonic specimens, no line of separation has been obse between the protoplasm at the deep end of the cone and the subst which occupies the axial part of the ommatidium proximal to the (compare Fig. 65). In attempting to determine the true relation, important to keep clearly in mind the fact that the proximal end of cone, usually bounded by a sharply marked line, is *not* the proximal of the cone cells ; but, as Watase ('90, Plate XXIX. Fig. 1) has well sh the cone is surrounded proximally as well as laterally by the protopla material of its cells. It is this material, not that of the cone pro which forms the proximal elongation.

I had hoped that by isolating the elements of the retina I could tain more conclusive evidence of the connection of these parts, but efforts were of no avail. My ill success was due, I believe, not to want of connection between the structures treated, but to the fact the material at my disposal had been kept so long in strong alcohol it had become unfit to serve for isolation. This conclusion seems to to be confirmed by the fact that I was unable even to isolate sati torily the retinulæ, structures which are usually separable with eas the fresh retinas of most Crustaceans.

If the view which I have set forth in the foregoing paragraphs cerning the interpretation to be put upon the axial part of the so ca rhabdome of Serolis be correct, it follows that the true rhabdome of Crustacean must be considered as composed of four rhabdomeres, of which is applied to the axial face of its appropriate retinular and that these four rhabdomes are prevented from uniting with another by a proximal extension of the cone cells which occupies axis of the ommatidium from the cone to the basement membra

Beddard ('84ª, p. 21), in his account of the eye in S. Schythei, st that the cone is "enclosed in a sheath of deep black pigment cells," Watase ('90, p. 294) has observed that in this genus there are two cells for each ommatidium. I believe that the number has been g correctly, for although I have not satisfactorily isolated the cells, I confident that I have identified their nuclei, and the number of the twice that of the ommatidia.

The nuclei of these pigment cells are most satisfactorily seen in

s (compare *nl. dst.*, in Figs. 65 and 69). In transverse
stage (Fig. 69) each cone is surrounded by a circle of
ch nucleus, however, participates in three adjoining cir-
ly there are only twice as many nuclei as ommatidia.
nuclei of these pigment cells (Fig. 60, *nl. dst.*) occupy
e positions as in the embryo; in the latter, however, they
ewhat hidden by the pigment which surrounds them.

yo the nuclei of the pigment cells surrounding the cone
losely, except in point of size, the nuclei of the retinular
nl. dst. and *nl. px.* in Fig. 65). In the nuclei of the
here is usually one distinct nucleolus, sometimes two, but
r particles. This condition also obtains in the nuclei of
lls. Not only are the nuclei of these two kinds of cells
nbryo, but they are also much alike in the adult (com-
Fig. 60 with *nl. rtn.'* in Fig. 63).

is resemblance, I believe that the pigment cells which
ne can be fairly considered to be modified retinular cells,
their sensory function in precisely the same way as in the
l retinular cells in Decapods (see Parker, '90^{a}, p. 57). If
ion of the pigment cells be accepted, it follows that in
ecapods, two kinds of retinular cells are present, proximal
hat the primitive ommatidium from which that of Serolis
bably contained six retinular cells functional as nervous
eed scarcely be added, that this number is characteristic
ia of many Isopods.

in the species of Sphæroma which I studied presents
hich suggests the differentiation of simple retinular cells
d distal cells. In Sphæroma there are seven retinular
Fig. 58); three of these are considerably reduced; the
are large, and recall the four retinular cells of Serolis.
ctions it can be shown that the four large cells in Sphæ-
esemble in appearance the four proximal cells in Serolis,
occupy the same relative positions in the ommatidium.
plane which separates the two cone cells of any given
nded, separates the four proximal retinular cells into two
cells each (compare Plate VI. Fig. 68 with Figs. 71 and
of separation in the cone of Sphæroma divides the retin-
hrough the single small retinular cell shown in the lower
8 (Plate V.) and *between* the two small cells on the oppo-
eparating the four large retinular cells into two groups,

The change which would convert an ommatidium like that in Sp roma into one like that in Serolis is easily imagined. It would co in the complete abortion of one of the three small retinular cells, and conversion of the other two into the pigment cells surrounding the c

In addition to the elements which have already been described in ommatidium of Serolis, there are certain small pigment cells which cur for the most part in the region of the retinulæ. Beddard (p. 21) describes these as long branching "connective-tissue cells name which might imply that they originated from the mesoderm, were therefore intrusive. Watase ('90, p. 293, Plate XXIX. Fig. 1) also described and figured these cells, but distinctly states his belief they are reduced ectodermic cells. In the adult I have observed in region of the cones, as well as near the retinulæ, certain small nu which are usually surrounded with more or less black pigment. Th I believe, represent the cells described by Beddard and Watase. In embryo certain scattered nuclei (*nl. h'drm.*, Figs. 65 and 70) occu the spaces between the ommatidia. It is probable that these nuclei ectodermic in origin, and I am at a loss to know what has becom them in the adult, unless they form the pigment cells already m tioned. I am therefore inclined to believe, with Watase, that the s additional pigment cells are reduced ectodermic cells.

The presence of the *hyaline* cells in the ommatidium of Serolis i Beddard has pointed out, almost a unique feature. These cells, usu two in each ommatidium, fill the space immediately below the rhabdo They are bladder-like (Fig. 62, *cl. hyl.*) and contain each a large g ular nucleus. Although it is stated that there are usually two of t cells in each ommatidium, I never found more than one to an omma ium in the several eyes of S. Schythei which I examined. This circ stance, however, is not surprising; for, as Beddard ('84^a, p. 22) remarked, the number of these cells is subject to variation, there b sometimes one, sometimes two, for each ommatidium. In S. Schy the single hyaline cell envelops more or less completely the distal of the fibrous portion of the cone cells, so that this part seems to pi the hyaline cell. A closer inspection, however, will usually show lines extending from the fibre to the periphery of the hyaline cell (c pare Fig. 62), and these lines indicate, I believe, the two walls of cell which have been infolded by the presence of the fibre during growth of the hyaline cell.

The source of the hyaline cells is not definitely known. Their nu (Fig. 65, *nl. hyl.*), as Beddard ('88, p. 450) has observed, are pre of embryos; and, although the cells may possibly be evidence on the whole favors the view that they are origin.

ctions have been attributed to the hyaline cells. Their n with what Beddard took to be the proximal extension me led him ('88, p. 450) to suspect that they might be tinular cells, but, as he (p. 451) further remarks, the fact fibres are connected with them opposes this view. Their uggested to him ('84^{a}, p. 22) that they might form a part apparatus; but it is difficult to understand, consider- on, precisely what that function would be. I am inclined h Watase ('90, p. 293), that they are chiefly concerned rt of the structures occupying the basal portion of the

a of S. Schythei many of the open spaces between the e basement membrane contain free non-pigmented cells g.). These have a distinct nucleus, finely granular pro- sharply marked outline. On account of the extreme va- which the different cells present, it is probable that when hibited amœboid motion. In appearance they correspond blood corpuscles of the body spaces, and as they occur not tina, but also in the rather large openings through the brane (compare Fig. 64), and in the space proximal to , I am of opinion that they are blood corpuscles.

rities which have led me to consider the ommatidium rately from that of other Isopods, are two: the posses- r more hyaline cells, and the presence of only four The latter peculiarity, as I have already shown, is not d; for in this genus, as in many other Isopods, the om- y contains six cells, although two of these, the distal ones, no longer functional as nervous structures. The other possession of hyaline cells, is not a very important char- as Beddard ('87, p. 235) has shown, these cells also occur it is probable, moreover, that they must be regarded as arged elements, specialized from among those cells which ds fill the spaces between the ommatidia. What dis- ommatidium in Serolis from that of other Isopods is, so much the possession of hyaline cells as the fact that lls are differentiated into two sets, proximal and distal.

In accordance with the facts already presented, the number of c contained in the ommatidium of Serolis can be stated as follows: c of the corneal hypodermis, two, with possibly two others interom tidial in position; cone cells, two; retinular cells, six, two distal four proximal; hyaline cells, one or two; a variable number of an pigment cells of ectodermic (?) origin.

Leptostraca.

The histological structure of the ommatidia in the Nebaliæ has b investigated, so far as I am aware, only by Claus ('88, pp. 65–84). have had no material for the study of the eyes in these Crustace and I can therefore only present, in the form of a summary, the m important results of Claus's exhaustive study.

In Nebalia there is a *corneal hypodermis* (Claus, '88, pp. 68 and 6 the cells of which are grouped in pairs. As in many of the hig Crustaceans, there is one pair of these cells for each ommatidium. *corneal cuticula* is facetted; the outlines of the facets are circular, and joining facets are separated from one another by a small amount of in vening cuticula (Claus, '88, Taf. X. Fig. 10). The *cones* are compo of four segments (Claus, '88, p. 69). The structure of the *retinul* somewhat complex. The greater part of the rhabdome is surroun by seven retinular cells. Distal to these cells, however, are seven ment cells, which enclose the proximal prolongation of the cone cells the distal end of the rhabdome. Such a relation between pigment and retinular cells is not of common occurrence among Crustaceans, it is possible that the bodies which Claus has taken for pigment cells really the distal ends of the retinular cells. Claus describes and fig what he believes to be the nuclei of both kinds of cells, but I th his figures fail to show that these nuclei are within the limits of cells to which they are said to belong. It seems to me quite poss that what he has described as two circles of seven cells each be merely one circle seen at two different levels, as the correspond in numbers suggests. This single circle would be of course comp of retinular cells, the nuclei of which are probably the distal one the two sets described by Claus. The proximal nuclei, which, acc ing to Claus, belong to the retinular cells, occupy positions not u quently taken by the nuclei of accessory pigment cells, and I am incl to think that such is their real nature. This interpretation would more in accordance with the conditions found in ommatidia which seven retinular cells than is the one given by Claus; but as I have tunity of studying the eyes in Nebalia, I can offer it of suggestion.

kinds of accessory cells are present in Nebalia; one of rom the corneal cuticula to the basement membrane, the nce of which is not so fully established, probably occurs ent membrane.

Cumaceæ.

hat is contained in Burmester's ('83, pp. 35–37) account te eyes in Diastylis (Cuma) Rathkii, nothing, I believe, finer structure of the eyes in the Cumaceæ. The speci- sposal for the study of these eyes proved upon examina- l. At least, the optic plates of all the individuals which th when studied from the exterior and when examined owed no evidence of eyes. My material consisted of iastylis quadrispinosa, G. O. Sars, and of three other un- cies, two of which belonged to the genus Diastylis and a. These were kindly sent me by Prof. S. I. Smith.

Schizopoda.

of Schizopod the eyes of which I have studied is Mysis h. Specimens of this Crustacean were kindly collected d's Holl, Mass., by Mr. C. B. Davenport. I am also s to Dr. H. V. Wilson, of the United States Fish Com- t my request sent me specimens of this species freshly üller's fluid.

the previous accounts of the eye in Mysis the nuclei *ypodermis*, although recognized, have been described as i. e. as nuclei of the cone cells. The differences between l nuclei and those of the cone cells can be easily seen in (Plate VII. Fig. 73). In this species the hypodermal lie in a plane somewhat nearer the external surface of he nuclei of the cone cells (*nl. con.*). In transverse sec- per levels, each ommatidium will be seen to contain two i (Fig. 75, *nl. crn.*) belonging to the corneal hypodermis, uclei (Fig. 76, *nl. con.*) in the cone. The hypodermal uch positions that the plane of separation between their at right angles to that between the cone cells (compare). The group of four nuclei, two belonging to the corneal hypodermis, and two to the cone cells, correspond without much do to the so called four Semper's nuclei mentioned by Claparède (' p. 194) in Mysis flexuosa, and described by Sars ('67, p. 33) in M. o lata. Nusbaum ('87, p. 179) also observed four similar nuclei in developing eye of Mysis chameleo, and Grenacher ('79, p. 118) descri the same number in Mysis vulgaris. In the last named species, acco ing to Grenacher, the four nuclei are grouped in two pairs, one of wh occupies a more distal plane in the ommatidium than the other. more superficial pair undoubtedly belongs to the corneal hypodermis, deeper pair to the cone cells.

It must be evident, then, that the nuclei of the cone cells and corn hypodermis have not always been carefully distinguished. In all ca where they have been separated, the corneal hypodermis has been sho to possess two nuclei for each ommatidium.

The *corneal cuticula* in Mysis, as Frey and Leuckart ('47^a, p. 1 first pointed out, is facetted, and the outline of the facet is a cir In Mysis stenolepis the circumference of the facet is tangential to circumferences of six adjoining facets (Fig. 74). In Mysis vulga Grenacher ('79, p. 118) has shown that the facet is not lens-like, but i uniform thickness throughout. In M. stenolepis, however, the cutic is often slightly thicker at the middle of the facet than at its edges (73, *cta.*). In this respect, therefore, different species probably vary.

The *cones* in Mysis vulgaris, according to Grenacher ('79, p. 118), composed of two segments. The same number is also present in cones of M. stenolepis (compare Figs. 76–78, *con.*). In longitudinal tions the cone (Fig. 73, *con.*) appears to consist of a uniformly and fin granular substance enveloped in a delicate but distinct membra Near the distal end of the cone the material which composes it beco more coarsely granular; in this the nucleus of the cone cell is usua lodged. Cones (Fig. 92) which have been isolated in macerating flu are plumper and apparently not so contracted as those which have b subjected to the process of cutting. The nuclei also are rounder and ful The cone proper (Fig. 92 *con.*) occupies a more central position in cone cells, and is surrounded by a finely granular material, which is pecially abundant at the proximal end. The difference between the c proper and this granular material was not generally observable in *secti* of the cones. In all of the many cones which I succeeded in isolati the proximal ends invariably had a broken appearance. Consequently believe that I have never completely isolated a pair of cone cells. question of the proximal extent of the cone I shall recur to later.

r *cells* in Mysis are of two kinds, proximal and distal. cells extend from the basement membrane distally to ich the cone rapidly contracts. The pigment which they the most part concentrated around the rhabdome, and upy a distal position in the cell (Fig. 73, *nl. px.*).

number of cells comprising the retinula is at least seven Possibly, as I have elsewhere suggested (Parker, '90ª, l number of cells in this retinula, as in that of Homarus,

determine this question, I have counted the number of l retinulæ of Mysis. The enumeration of these can be in Figures 79 to 82. These figures represent successive ons through four ommatidia, in the region occupied by tinular nuclei. The axis of each ommatidium is marked portion of the cone cells (*cl. con.*), and the same ommanated in different sections by the same Roman numeral. ommatidium II. can be counted the most readily. In ch represents the most distal section of the series, the idium II. is surrounded by a circle of six nuclei, which bered from 1 to 6. Each of these nuclei, however, paree circles (compare nucleus 5), and hence only two of the rred to ommatidium II. Two similar circles occur, one shown in Figure 80, and one in that shown in Figure 81. r instance, two nuclei in each circle belong to omma- these three circles, then, there are in all six nuclei to be atidium II. In addition to these nuclei, it will be no- the right of the cone in Figure 80 there is one more), and still another in a similar position in Figure 82. lei, when added to the six already summed up for om- nake a total of eight nuclei for this ommatidium.

mber of nuclei occurs in each of the other three omma- arrangement is not quite so regular as in the one just n this I conclude that the number of nuclei in a retinula nt.

nuclei in this retinula usually present a very uniform he most proximal one differs somewhat from the others elongated (compare Figs. 73 and 82). The seven distal nt of their general resemblance, belong, I believe, to the l retinular cells. The single proximal nucleus probably eighth rudimentary cell. The position of this nucleus, proximal to the other retinular nuclei, is similar to that occupied b nucleus of the rudimentary retinular cell in Homarus (compare P '90ª, pp. 20, 21).

The *rhabdome* in Mysis stenolepis lies in the proximal portion retina. It is rather stout, blunt at its distal end, but sharper mally (Fig. 90). Its surface is marked with coarse corrugation transverse section, its outline is a square; this is subdivided b lines into four smaller squares, a condition already observed by cher ('79, p. 119) in M. flexuosa. The relation of the retinula to these divisions of the rhabdome can be clearly seen in Figure 8

According to Grenacher's account ('79, p. 118), a rod-like str extends, in Mysis vulgaris and M. flexuosa, through the axis ommatidium from the distal end of the rhabdome to the region proximal retinular nuclei. Whether this rod be a proximal contin of the cone, or a distal extension of the rhabdome, Grenacher fo difficult to decide. He is inclined, however, to the former opinion.

A similar structure occurs in the ommatidia of Mysis sten Although I have made repeated attempts, I have never succee isolating the rod in connection with either the rhabdome or the cells. In transverse sections, the distal end of it appears in a p slightly proximal to the retinular nuclei (Figs. 73 and 83). The cells extend proximally as a transparent axis to this region, an most distal indications of the rod are four fibres which lie o periphery of what I take to be the proximal end of the cone (Fig. 83). Somewhat deeper than this, the four fibres thicke finally fuse (Fig. 84), producing a body which in transverse secti the outline of a four-pointed star. In a plane slightly more pro the outline changes to a squarish one (Fig. 85), and this is re almost to the proximal end of the rod. Throughout its exten problematic rod is closely surrounded by the seven proximal re cells (Fig. 85). It is separated from the rhabdome by what app be an open space (Fig. 90, at the level of the dotted line 86). In verse sections (Fig. 86), however, this space is seen to be divid delicate membranes into four compartments.

These facts, however, do not aid much in deciding the relati of the rod. The fact that it shows indications of being compo four parts suggests its connection with the rhabdome. The four of which it consists do not, however, correspond in position to t ments of the rhabdome, but fall between them. (Compare Figs. 87.) On the other hand, if it were an extension of the cone, one

composed of two, instead of four parts. Its position, how-
ich is more frequently occupied in other Crustaceans by
sion of the cone cells than by a process from the rhab-
twithstanding its division into four parts, I am inclined
Grenacher, and to regard it as belonging to the cone cells
e rhabdome.

etinular cells in Mysis surround the lateral faces of the
3, *cl. dst.*). Apparently they reach the cuticula; their
are attenuated and become lost in the region of the
roximal cells. Their pigment is limited to their proximal
nsists of a distal layer of brownish material, proximal to
h more extensive deposit of blackish granules. Each cone
by six of these cells, as can be seen from their outlines
t.), and still more satisfactorily from the arrangement of
ig. 75, *nl. dst.*). Each cell, however, participates in three
quently, there are only twice as many of these cells as

each distal retinular cell is occupied by a transparent
transverse section has the appearance of a light spot
depigmented sections stained with Kleinenberg's hæma-
rods are deeply colored (Fig. 78). I shall recur to their
ficance.

t which is found in the region of the rhabdomes in Mysis
: blackish granules, and a fine flaky material, white by
yellowish by transmitted light. The black granules are
art contained in the retinular cells. The lighter pigment
ciated with certain nuclei, two of which are shown in
ms'drm.). These nuclei are closely invested by the pig-
bably belong to the cells in which the pigment is con-

of the yellowish pigment cells is not easily determined.
ey are not limited to the retina, but also occur in the
. At least these spaces contain masses of pigment and
n all essential respects are similar to those distal to the
mpare the two nuclei, *nl. ms'drm.*, Fig. 90). In one case
f one of these cells was found apparently caught in its
h an opening in the basement membrane (Fig. 91). For
I believe that the yellowish pigment cells on the two sides
ane have had the same origin. The question as to the
yellowish pigment cells in the retina, therefore, appears

to me to involve that of the origin of the similar cells beneath the retina. If I am right in this conclusion, all these cells must either have arisen in the retina, many of them migrating in a proximal direction out of it, or they must have had some extra-retinal origin, some of them migrating into it. On account of the considerable numbers in which they exist in the spaces below the retina, it seems to me much more probable that they have had an extra-retinal origin than that they have come from the retina itself. If this is their source, it is evident that those which are in the retina are intrusive. The nucleus which has already been mentioned as caught in an opening of the basement membrane (Fig. 91) has more the appearance of a body which is making its way into the retina than of one which is moving in the reverse direction, and may therefore be regarded as confirming to some extent the view of the extra-retinal origin of these cells. Their source, however, cannot be stated with certainty. Their power of migration implies amœboid activity, and this might be taken as an indication of their mesodermic origin.

The following cells characterize the ommatidium of Mysis: cells of the corneal hypodermis, two; cone cells, two; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory pigment cells (mesodermic ?) present.

Stomatopoda.

The material which I have had for the study of the eyes in the Stomatopods consisted of two specimens of Gonodactylus chirarga, Latr. These were kindly given me by Mr. W. S. Wadsworth, who had collected them in the Bermudas. One of them had been killed in hot water and preserved in alcohol; the other was both killed and preserved in strong alcohol; both were in excellent histological condition.

In Gonodactylus, as I have previously mentioned, there are two kinds of ommatidia; these differ in no important respect except size.

Longitudinal sections of both kinds are represented on Plate VIII.; the figure of the larger kind (Fig. 94) is taken from a depigmented section, that of the smaller one (Fig. 95) from a section containing the pigment in its natural condition. In the following description I shall give an account of the structure of the larger ommatidia, alluding to the condition of the smaller ones only when it differs in some important respect from that of the others.

The *corneal hypodermis* is represented in the ommatidium of Gonodactylus by two cells, the nuclei (Figs. 94–96, *nl. crn.*) of which can easily. Directly under the corneal cuticula each pair of ls is in contact with similar pairs belonging to adjoining hat the layer here forms a continuous sheet. In a more the neighboring pairs of hypodermal cells are not in con- Fig. 93, a tangential section in which the extreme right- esents the condition immediately below the cuticula, while e left represent central portions successively more proxi- . The only indication of a separation between the two hy- of each pair is seen in the distal projection of the cone o hypodermal nuclei (compare Figs. 94 and 96, *con.*).

uticula in Gonodactylus is facetted, but the proximal and the facets are apparently plane. Over the smaller om- ets are hexagonal in outline, whereas over the larger ones gular, and their arrangement is often indicative of the em. In Squilla mantis, according to Will ('40, p. 7), the gonal.

Gonodactylus are composed for the most part of a uni- r substance. Distally, they are pointed and probably eal cuticula; proximally, they terminate at the rounded dome (Fig. 94). Each cone contains in its distal enlarge- ei (Fig. 97, *nl. con.*), two of which lie directly proximal the corneal hypodermis, while the remaining two alter- (compare Figs. 96 and 97). The proximal part of the longitudinally into four segments (Fig. 98). Each seg- led distally, would include one of the four nuclei, and one of the four cells by which the cone was produced. tis, according to Steinlin ('68, p. 17), the cone is also ur segments.

r cells of Gonodactylus are of two kinds, proximal and oximal cells, constituting the retinula itself, surround the letely, and extend distally only a short distance beyond They contain only a small amount of pigment, which is two regions, at their distal ends and near the basement e rhabdome is surrounded throughout its length by a dense layer of pigment. This layer is more extensive ommatidia (Fig. 102) than in the larger ones. The proximal retinular cells (Figs. 94 and 95, *nl. px.*) are eir distal ends.

of cells in the retinula of Squilla, as described by Grena- 3) and by Hickson ('85, p. 341, Fig. 2), is seven. In

Gonodactylus (Fig. 101) the retinular cells are certainly as nume as in Squilla; but seven obvious cells in the retinula, as I have alr shown in Mysis, may suggest the presence of eight in all, one of t being rudimentary. This condition is in fact characteristic of Gonc tylus also, as can be seen in the series of ommatidia shown in Fig. These six ommatidia represent consecutive individuals in one of bands of larger ommatidia previously mentioned. The band as a w is cut obliquely, and in such a way that the ommatidia from 1 to 6 cut successively in deeper or more proximal planes. In ommatidiu the rhabdome is surrounded by seven retinular cells, four of which upon the right side and three upon the left. In addition to the large nucleus (*nl. px.*) lies close to the rhabdome. Ommatidium 2 essentially the same structure as ommatidium 1. In ommatidium 3 nucleus corresponding to the one seen in ommatidium 1 and 2 is no lo visible, but in its stead there is a small mass of granular protopl A similar mass is also seen in ommatidia 5 and 6. It is usually ent directly proximal to the nucleus figured in ommatidia 1 and 2, is, I believe, the protoplasmic body of the cell to which this nuc belongs. In ommatidium 4, the seven nuclei of the seven large (f tional) retinular cells can be seen. These nuclei appear very larg transverse section compared with the cells in which they occur. probable that the cell wall is distended by them, although, owing to indistinctness of the cell boundaries, I have not obtained positive dence of this. In ommatidium 6 the seven retinular cells are seen section at a plane proximal to that in which their nuclei lie. A ommatidium 1, three of them are upon one side of the rhabd and four upon the other. In a part of the ommatidium more pr mal than that shown in number 6 (Fig. 100), the transverse sec of the retinula has the appearance seen in Figure 101. Here retinular cells have the same relation to the rhabdome that they d ommatidium 6 (Fig. 100), except in the case of the upper right-h cell of that figure. This cell enlarges in its more proximal portion, comes to occupy a position directly below the cell whose nucleus is sh in ommatidium 1 (Fig. 100). The gradual disappearance of this di cell as one proceeds in a proximal direction from the plane of num 6, Figure 100, to that of Figure 101, and the gradual shifting in position of the cell which replaces it proximally, can be followed easily that there is not the least question as to the accuracy of relations described. It is evident, then, that in Gonodactylus, as in My the retinula consists of eight cells, one of which is rudimentary.

e (Figs. 94 and 95, *rhb.*) in Gonodactylus is an elongated ire of uniform thickness, which extends from the region l retinular nuclei to the basement membrane. It shows thed edge (Fig. 94), especially in specimens which have th potassic hydrate. In transverse section it is squarish. nall size, the exact relation of the seven surrounding cells s cannot be easily determined. The single unpaired cell ainly lies opposite a face, not an angle. In this respect the unpaired cell in Squilla as figured by Grenacher ('79, 22). Probably in Gonodactylus the remaining six cells the sides of the rhabdome as the corresponding ones are pare Grenacher's Fig. 122). In Gonodactylus the retinu- habdome are in close contact with one another. The ese elements as figured by Grenacher in Squilla is prob- as Grenacher himself suggests. In Squilla, according to ('68, p. 17) and Grenacher ('79, p. 125), the rhabdome ections is subdivided into four equal parts, somewhat as ve not observed this condition in Gonodactylus.

etinular cells in Gonodactylus occupy the usual position . They contain very little pigment, and their number ned only by that of their nuclei. These agree with the roximal cells in the possession of a single well defined h is most readily seen in depigmented sections (compare *px.* in Fig. 94). The distal nuclei, especially in the larger ommatidia, are arranged in rows which alternate of cones (Fig. 99, *nl. dst.*). Although the nuclei are not arranged, they often show a tendency to be grouped in e pairs are so placed that in each row there is evidently djacent ommatidium. Moreover, in equal lengths of ad- nuclei and cones, the nuclei are always double the num- I am convinced by these facts that there are two distal for each ommatidium.

cells already described, certain others occur in the proxi- e retina in Gonodactylus. These are represented by a gated nuclei (Fig. 94, *nl. ms'drm.*), which are very similar to certain nuclei occurring in the spaces below the base- e. I therefore believe that in Gonodactylus, as in Mysis, ortion of the retina is occupied by intrusive cells, which esodermic in origin.

f cells found in the ommatidium of Stomatopods are as follows : cells of the corneal hypodermis, two ; cone cells, four ; pr mal retinular cells, eight, one of which is rudimentary ; distal retin cells, two ; accessory cells (mesodermic ?) present.

Decapoda.

I have studied the eyes of the following species of Decapods : Gel mus pugilator, Latr. ; Cardisoma Guanhumi, Latr. ; Cancer irrora Say ; Hippa talpoida, Say ; Palinurus Argus, Latr. ; Pagurus longicar Say ; Homarus americanus, Edw. ; Cambarus Bartonii, Fabr ; Cran vulgaris, Fabr. ; and Palæmonetes vulgaris, Say. I collected much this material at the Station of the United States Fish Commission Wood's Holl, Mass. The specimens of Cambarus were obtained in vicinity of Philadelphia. I am under obligations to Mr. Herbert Richards for specimens of Palæmonetes collected by him at Newp R. I. A number of eyes of two Crustaceans, Cardisoma and Palinu were kindly obtained for me by Mr. Isaac Holden ; they were collec on the coast of Florida by Mr. Ralph Munroe, to whom I am indeb for the careful way in which they were preserved.

The *corneal hypodermis* in Decapods was first recognized by Pat ('86, pp. 626 and 642), who observed it in Penæus, Palæmon, Pagu and Galathea. Since Patten's announcement of the presence of layer in Decapods, it has been identified in a number of other gene in Crangon by Kingsley ('86, p. 863), in Alpheus by Herrick ('86, p. in Astacus by Carrière ('89, p. 225), in Cambarus and Callinectes Watase ('90, pp. 297 and 299), and in Homarus by myself ('90^a, p. More recently I have observed it also in Palæmonetes (Plate IX. 103, *cl. crn.*), Crangon, Cambarus, Palinurus, Pagurus, Hippa, Can and Cardisoma.

In almost all Decapods in which the arrangement of the cells in corneal hypodermis has been observed, these elements have been fo to be grouped in pairs, and so distributed that each pair occupies distal end of an ommatidium (compare Figs. 103 and 106, Plate I This arrangement has been observed, either by others or by myself the genera mentioned in the preceding paragraph, except Callinec in which the exact arrangement of the cells has not been recor Reichenbach's statement ('86, p. 91), that in Astacus there are f hypodermal cells under each facet, is probably erroneous, as Carriè observations show.

Although Patten was the first investigator who clearly demonstra the presence of the corneal hypodermis in Decapods, Grenacher, in 18

elieve, the nuclei of this layer, without however correctly
hem. In his account of the ommatidium in Palæmon,
9, p. 123) mentions two kinds of bodies in what he takes
l ends of the cone cells. Of these, the more distal ones
117, *n.*) represent, in his opinion, the nuclei of the cone
e proximal (Fig. 117, Kk^1.) he considers as differentiated
cone itself. The positions occupied by these bodies in
by certain bodies which I have observed in Palæmonetes
. 103), are so similar that I believe the structures in the
be homologous. In Palæmonetes the distal bodies lie in the
rneal hypodermis (Fig. 103 *cl. crn.*), and are the nuclei of
hey represent what Grenacher considered the nuclei of the
alæmon. The proximal bodies in Palæmonetes (Fig. 103,
nquestionably the nuclei of the cone cells, yet they corre-
Grenacher considered the four pieces of the distal segment
I therefore believe that what Grenacher has described as the
cone cells are really the nuclei of the corneal hypodermis,
he considered distal segments of the cone are the nuclei
lls.

cuticula in Decapods, in correspondence with the differ-
tion of the corneal hypodermis, is facetted. The outline
s either hexagonal or square. The particular genera in
ifferent kinds of facets occur have already been mentioned
h the arrangement of the ommatidia in Decapods. The
acets in Decapods are usually very nearly plane, but in
rding to Grenacher ('79, p. 123), and in Palæmonetes
. 103, *crn.*) according to my own observations, the facets
iconvex. In Homarus, as Newton ('73, p. 327) has ob-
n Astacus according to Carrière ('85, p. 167), the distal
facet is plane, the proximal slightly convex. In even
eme cases, however, the convexity of the facets in Decapods
t to make them very effective as lenses.

n Decapods are generally bisected by a fine straight line.
Patten has suggested, probably represents the plane of
ween the two subjacent hypodermal cells. In the square
ne either divides the facet diagonally, as in Homarus
Fig. 2), or transversely, as in Palæmonetes (Plate IX.
the hexagonal facets it either bisects opposite sides, as in
X. Fig. 126), or unites opposite angles, as occasionally in
ten, '86, p. 644, Plate 31, Fig. 114). Leydig's ('57, p. 252,

Fig. 134) figure of Astacus, in which each facet is subdivided by
diagonal lines into four areas, and Newton's ('73, p. 327) state
that the same condition occurs in Homarus, are probably incorrect.

The *cones* in Decapods are composed of four segments. This nu
was first observed by Will ('40, p. 13) in Palæmon, and has since
recorded in many other genera. So far as I am aware, there ar
Decapods in which the number of segments is not four. As Clapa
('60, p. 194) first pointed out in Galathea and Pagurus, each seg
contains a nucleus and represents a single cell. Although the si
cance of these nuclei was without doubt first fully appreciate
Claparède, it is probable that they were previously seen by Le
('55, Taf. XVII. Fig. 31) in the crayfish.

As a rule, the distal termination of the cone cells is on the prox
side of the corneal hypodermis. In the lobster, however, and in P
monetes (Plate IX. Fig. 104), the pointed ends of these cells
between the two cells of the corneal hypodermis, and probably
in contact with the corneal cuticula near the middle of a facet.

It is difficult to determine with accuracy the proximal terminatio
the cone cells. They can be easily traced to a region immediately c
to the distal end of the rhabdome. In this region, as Schultze
Taf. I. Figs. 9 and 11) has clearly demonstrated in Astacus, the fib
ends of the four cone cells separate, and pass partially around the r
dome. In Homarus, these fibres extend proximally, and finally
minate at the basement membrane. A similar method of termina
also occurs in Palinurus. In the other genera which I have studied
fibres, although visible near the distal end of the rhabdome, are lo
the adjacent tissue, and I do not know whether they terminate in
tissue without special attachment, or whether they make their wa
excessively fine fibres to the basement membrane. The separatio
the fibrous ends of the cone cells, near the distal end of the rhabd
has been observed by Steinlin ('66, p. 93) in Palæmon, and by Sch
('67 and '68) in several other Decapods. The statement made by m
of the older investigators, and recently reaffirmed by Patten, that
cone and rhabdome are parts of one continuous structure, is wit
doubt incorrect.

The resolution of the *retinula* into its cellular constituents was
attempted in Decapods by Leydig ('55, p. 408), according to whom
retinula of Herbstia contains four cellular bodies, the nuclei of w
can be distinguished in the distal part of the structure. A some
similar condition was described by Newton ('73, p. 333) for Homa

, as in Herbstia, it was maintained that there were only
ıbsequent investigators have not confirmed this conclusion.
sections of the retinula of Palæmon, Grenacher ('77, p. 32)
ıted that the rhabdome is surrounded by *seven* retinular
ɔ ('77, p. 33, and '79, p. 125) observed the same number
læ of Astacus and Portunus. Since the publication of
ɔbservations, a retinula containing seven cells has been
us by Carrière ('85, p. 169), in Penæus, Palæmon, Gala-
urus by Patten ('86, pp. 630 and 643), and in Cambarus
)0, p. 299).

s, as I ('90ᵃ, p. 21) have already shown, the retinula con-
ion to the seven functional retinular cells, an eighth rudi-
which is little more than a nucleus. In order to ascertain
ɔr absence of this eighth cell in other Decapods, I have
to record the number of retinular nuclei, as well as the
ıctional retinular cells. In some genera, such as Cardisoma
ıave not been able, on account of the unfavorable condition
o make this determination; but in Palæmonetes, Palinurus,
angon, and Cancer, I have succeeded in ascertaining the
of the functional cells and of the nuclei in the retinulæ.

netes each rhabdome is surrounded by at least seven re-
(Plate IX. Fig. 114, *cl. px.*). The nuclei of these cells
ghtly distal to the rhabdome (Fig. 104, *nl. px.*). Their
s shown in Figures 110, 111, and 112, which represent a
ecutive sections through the region occupied by the prox-
r nuclei of five ommatidia. The nuclei of the different
e arranged upon the same plan, and the corresponding
lifferent sets have been marked by the same number. In
ces, nuclei have been cut in two, and their parts are found
sections; in such cases the separate portions have been
the same number. As can be seen in these figures,
f nuclei in the distal portion of each retinula is seven.
on to these, there is also another one, which occupies a
the rhabdome. This nucleus resembles the others in all
t that it is somewhat longer and narrower. It is drawn
at the level marked 114, and in Figure 114 one can see
with which it occurs. This nucleus is the eighth in the
læmonetes, and since it differs somewhat in structure from
n, and occupies a more proximal position, I believe it rep-
mentary retinular cell.

In the distal portion of the retinula in Cambarus there are eight nuclei. The arrangement of these, as seen in successive transverse sections, is shown in Plate X. Figs. 118 to 122. In Figure 118, which represents the most distal section of the series, there are four nuclei, and these are so arranged that there is evidently one for each ommatidium.[1] In the next section (Fig. 119) there are seven nuclei, none of which were seen in Figure 118; the place for an eighth is indicated by an open area, and the eighth nucleus itself is seen somewhat out of place in Figure 120 (*x*). Four of the eight nuclei belonging in Figure 119 are arranged in a manner similar to those in the preceding section, but are not to be confounded with them. The remaining four are so placed that there are two for each ommatidium. Hence in this plane there are, as a whole, three times as many nuclei as there are ommatidia. In the next section (Fig. 120), omitting the nucleus marked *x*, which has been recorded as belonging to the preceding section, there are four nuclei, so arranged that there is one for each ommatidium. In the following section (Fig. 121) the nuclei, omitting the one marked *x*, which will be considered as belonging to the next following section, are so arranged that there are two for each ommatidium. In the last section (Fig. 122), the nuclei are not so regularly grouped as in the previous section, but when taken with the nucleus marked *x* in Figure 121, they constitute a group of four, the arrangement in which is such that each nucleus is intermediate between *four* groups of cone cells rather than between *two*, and therefore in the plane of this section there is one nucleus for each ommatidium. From this enumeration it is evident that the total number of retinular nuclei is eight; namely, one in the first section, three in the second, one in the third, two in the fourth, and one in the fifth. The structure i affords no clue as to which one belongs to the rudi-

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[1] The nuclei shown in Figures 118 to 122 are arranged upon either the plan shown in Figure 118 or that in Figure 121 (omitting nucleus *x*). Imagine the arrangement in Figure 118 extended over a large surface. The groups of four cone cells could then be regarded as forming lines in the direction of the length of the plate. These lines would alternate with lines of nuclei, and as the nuclei in any line would alternate with the groups of cone cells in an adjoining line, the number of nuclei must equal exactly the number of groups of cone cells; i. e. in this arrangement there is one nucleus for each ommatidium. In a similar way, alternating vertical lines may be constructed from the arrangement in Figure 121. One line would be composed entirely of nuclei situated one opposite each group of cone cells; the other, of alternating nuclei and groups of cone cells. In the former, as well as in the latter, there would be as many nuclei as groups of cone cells. Hence, in this arrangement the nuclei are twice as numerous as the groups of cone cells; i. e. there are two nuclei for each ommatidium.

s (Plate X. Fig. 125, *nl. px.*), the eighth nucleus is regu-
and easily seen. In Cancer (Fig. 129, *nl. px. 8*) it occu-
between the adjacent retinulæ. It can also be identified

e in Decapods, according to all recent observers, contain
ıal cells. In Homarus, Palinurus, Cambarus, Crangon,
and Cancer, the retinulæ contain, in addition to the
f the functional cells, an eighth nucleus, which repre-
e, a rudimentary cell. It is probable, therefore, that in
each retinula really contains eight cells, one of which is

ne in Decapods presents a very uniform structure. It is
ngated body, pointed both at its distal and its proximal end,
covered, except at its distal tip, by the proximal retinular
e Decapods in which it is large enough to be conveniently
ransverse section is squarish, and usually subdivided by
nes into four smaller squares (Plate IX. Fig. 113). As
, pp. 31, 32) first demonstrated in Palæmon, the retinular
r peculiarly arranged around the rhabdome. One of its
nked by *one* cell, the other three by two cells each. This
an be seen in Palæmonetes (Fig. 113), and probably obtains
ds.

s Argus (Plate X. Fig. 124) there appears to be no rhab-
the translucent axial portion of each retinular cell can
esent segments of it. The fibrous ends of the cone cells
be easily identified between the retinular cells, but the
etinula is filled with pigment, and shows not the least trace
e. This peculiarity of Palinurus was noticed as early as
('40, p. 15), who described the ommatidium in this genus
ut a transparent mass (= rhabdome).

ie *distal retinular* cells in Decapods were collectively rec-
iller ('26, pp. 355, 356) some sixty years ago as a definite
in the distal portion of the retina in the crayfish, they
ified as separate cells until quite recently. The first in-
bserve them was Carrière ('85, p. 169), who described
ıs as a pair of pigment cells flanking each cone. In Cam-
, and Homarus, they also cover the sides of the cone, and
ned genus they are produced proximally into long fibres,

which perhaps pass through the basement membrane. In Palæmo (Plate IX. Fig. 108, *cl. dst.*) and in Cancer (Plate X. Fig. 127, *cl.* they are reduced to pigmented threads, which, starting from comparat large bases, twine around the lateral surfaces of the cones.

The arrangement and number of the distal retinular cells can be readily determined from their nuclei. In Cancer (Plate X. Fig. the cells are arranged in circles of six around each group of cone each cell, however, participates in three circles, and consequently are in reality only twice as many cells as ommatidia. This arrange of the cells also occurs in Cardisoma, Hippa, and Pagurus. In Cra (Fig. 123), as I have previously remarked, the nuclei of the distal re lar cells are arranged in rows alternating with the rows of cones. T are twice as many nuclei as cones; hence I conclude that here there are two distal cells for each ommatidium. In Homarus, Palin Cambarus, and Palæmonetes (Plate IX. Figs. 103 and 109, *nl. dst.* nuclei are grouped distinctly in pairs, one pair for each ommatidiun

Each cone in Penæus, according to Patten ('86, p. 634), is surrou by two pairs of pigment cells, and Watase ('90, p. 299) states th Cambarus the dioptric part of the ommatidium is sheathed by *fou* ment cells. In Cambarus Bartonii I have been able to find onl such elements, the pair of distal retinular cells already described, a the other Crustaceans which I have studied I have observed no which supports Patten's statement concerning the four pigment ce Penæus. I am therefore inclined to doubt the accuracy of these observations.

The interommatidial space in the basal part of the retina in monetes contains a light pigment similar to that described in the r of Mysis. Like this the pigment in Palæmonetes is white by refl light, and yellowish by transmitted light (compare Plate IX. Fig. It is apparently contained within cells (Fig. 103, *cl. ms'drm.*) whose lines are very irregular, and whose nuclei (Fig. 104, *nl. ms'drm.* small and somewhat variable in form. These cells occur on both si the basement membrane. As in Mysis, they have probably mig into the retina, and are perhaps mesodermic in origin. They have seen by Carrière ('85, p. 169) in Astacus, by Patten ('86, p. 63 Penæus, and by myself ('90^a, p. 25) in Homarus. I have also rec observed them in Crangon, Cambarus, Cardisoma, Pagurus, and nurus, as well as in Palæmonetes.

From what has preceded it is evident that the ommatidium in pods contains the following elements: cells of the corneal hypode ls, four; proximal retinular cells, eight, one of which is distal retinular cells, two; accessory cells, mesodermic (?) present.

Table of Ommatidial Formulæ.

concluded my account of the structure of the ommatidia s, and for the purpose of presenting in a condensed form rtant features I have devised the following table. This series of ommatidial formulæ constructed upon the plan described in the Introduction. The figures indicate the rticular kinds of cells present in the ommatidium of a The abbreviation *pr.* (present) marks the presence of any hen the number of that kind is not constant for different the same individual.

OWING THE CELLULAR COMPOSITION OF THE OMMATIDIAN
CRUSTACEANS.

ustaceans.	Cells of Corneal Hypodermis.	Cone Cells.	Retinular Cells.			Accessory Cells.
				Differentiated.		
			Undifferentiated.	Proximal.	Distal.	
	pr.	2	5			pr. (ect. ?)
and Apusidæ,	2	4	5			0
	pr.	5 (4)	5			0
	?	5	5			pr. (ect. ?)
ella, hirina, lus,	pr. ? pr.	2 ? 4	5 3 5			pr. (ect. ?) ? ?
 io, 	2 2 2 (+?)	2 2 2	6 7 	 4	 2	pr. (ect. ?) pr. (ect. ?) pr. (ect. ?)
	2	4	7			pr. (ect. ?)
	2	2		7 + 1	2	pr. (mes. ?)
	2	4		7 + 1	2	pr. (mes. ?)
	2	4		7 + 1	2	pr. (mes. ?)

res in the table require explanation. Among the number ed for the Estheridæ, the figure within the parenthesis under the head of Cone Cells indicates the occasional occurrence of cones containing only four cells, although the usual number is five. In the line for Serolis, under the head of Corneal Hypodermis, the parenthesis and included signs are intended to indicate the possibility of there being more than two cells in the corneal hypodermis for each ommatidium. In the Schizopods, Stomatopods, and Decapods, the number of proximal retinular cells is expressed in the form of 7 + 1 instead of 8, because one of the cells is rudimentary.

THE INNERVATION OF THE RETINA.

The innervation of the retina in the compound eyes of Crustaceans is chiefly interesting, because of its importance in relation to physiological questions. As this paper deals with a morphological topic, it would be obviously irrelevant to enter upon any extended discussion of this subject. Nevertheless, the innervation of the retina is not without some bearing on the general question which I have set for myself, and I shall therefore not pass it by, but put in as brief a form as possible what I have observed concerning it.

In my account of the retina in the lobster, I described the optic-nerve fibres as terminating in the proximal retinular cells. Near the ganglion each fibre consists of a bundle of fibrils, simply enclosed within a sheath, but as it approaches the retina it becomes coated with pigment. The pigment increases in quantity and the fibre correspondingly enlarges till it finally becomes continuous with the deeply pigmented retinular cell. The fibrillar axis can be distinguished in the pigmented portion of the fibre as a transparent axial structure, and it can also be traced distally through the pigment of each retinular cell till it breaks up into its ultimate fibrillæ, which are spread over the distal half of the rhabdome. This is the method of nerve termination in the lobster, and points very conclusively to the rhabdome as the terminal organ.

What I have seen of the termination of the nerve fibres in other Crustaceans confirms the account which I have already given for the lobster. In some species which I have studied, owing to the small size of the retinal elements, I was unable to determine the cells with which the nerve fibres connected. The termination of the fibres in the cells of the retinula was observed, however, in the following genera: Branchipus, Limnadia, Pontella, Gammarus, Talorchestia, Idotea, Porcellio, Sphæroma, Serolis, Gonodactylus, Mysis, Palæmonetes, Crangon, Cam-

us, Pagurus, Cancer, and Cardisoma. In the majority of
r axis could be distinguished.[1] In Cambarus, as in Homa-
fibrillæ spread over the distal portion of the rhabdome.
exceptionally interesting condition is presented. At the
sement membrane each retinular cell contains a large fibril-
VI. Fig. 64, *ax. n.*). This becomes somewhat subdivided
stal portion of the cell, and in the region of the retinular
represented by a cluster of several smaller axes (Fig. 63).
f the hyaline cell, these however cannot be distinguished
the scattered condition of the pigment granules in this
bly to be accounted for by the presence of many separate
substance of the cell. In the region of the rhabdome an
ber of fine lines can be seen extending from the retinular
ubstance of each rhabdomere (Fig. 61). These, I believe,
fibrils of the nervous axis. They have been previously
erolis by Watase ('90, p. 291), and are so readily visible
be no question as to their presence. Each fibril is per-
the longitudinal axis of the ommatidium, and extends
habdomere to its axial surface. Before reaching this,
fibril passes through what seems to be a delicate mem-
closely examined, this membrane often has the appearance
s instead of a line, and in several cases I have been unable
traces of it. What its significance is, I am at a loss to
e previously observed, when the elements of the retinula
the rhabdomere shows no tendency to break along this line.
cture is pierced by the fibrils, and does not appear to be
e of rupture, and since sometimes it is apparently absent,
y be considered, from a morphological standpoint at least,
y and rather unimportant modification within the rhabdo-

ect in maintaining that the nerve fibrils in Serolis terminate
mère, it is probable that they have a similar method of
other Crustaceans, and in such instances as Homarus,
ve been traced only to the surface of the rhabdome, their
tion has probably not been seen.

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brillar axis was traced from below the basement membrane to the
bdome in Gammarus (Plate I. Figs. 6–8), Porcellio (Plate V. Fig.
e V. Figs. 53 and 55–57), Mysis (Plate VII. Figs. 87–89), Gono-
VIII. Figs. 101, 102), Palæmonetes (Plate IX. Figs. 116, 117), Cam-
Cancer (Plate X. Figs. 130 and 131), and Cardisoma.

The termination of the fibrillæ of the optic nerve in the rhabdome supports Müller's belief that the nerve fibres terminate in a region near the proximal ends of the cones, and Grenacher's more specific view that they are connected with the retinular cells, and that the rhabdome is the terminal organ. This method of termination is not consistent with the opinion of Gottsche and Leydig, that the cone is the terminal organ, nor with Patten's rather similar belief that the ultimate nerve fibrillæ are distributed to the cone. I am therefore compelled to think that these authors are mistaken in their conclusion.

THEORETIC CONCLUSIONS.

In attempting to account for the variation in the number of cells in different types of ommatidia, two courses naturally suggest themselves. Either the different kinds of ommatidia vary in the number of cells which they contain, because they have had separate origins, or they are different because in some or all of them the ancestral ommatidium has suffered modification. An examination of the table on page 115 shows conclusively, I think, that in Crustaceans even the most extreme types are so little removed from one another that it is much more probable that the different kinds of ommatidia are genetically connected, than that they have been produced independently. Granting this statement, the question naturally arises, What are the means by which the primitive ommatidium was modified? I believe that a close scrutiny of the cellular structure of the ommatidia in living Crustaceans will disclose some of the factors in this process. There are at least three of these to be distinguished: the differentiation of cells, the suppression of cells, and the increase in the number of cells by cell division.

By the differentiation of cells, I do not mean the process by which hypodermal cells have become converted into retinular or cone cells, but that by which an element already differentiated in the ommatidium is secondarily modified to subserve another function. The only instance of this kind with which I am acquainted occurs among the retinular cells. In the majority of the simpler Crustaceans, the sides of the cones are covered with pigment, which is almost always contained in the distal ends of the retinular cells. In Serolis, among the Isopods, and apparently in all the genera of Stomatopods, Schizopods, and Decapods, the cones are surrounded by special pigment cells. These are always twice as numerous as the ommatidia, and represent, I believe, retinular cells which have become differentiated for the special purpose of sheathing

e way in which this differentiation may have occurred
n suggested in my paper on the lobster ('90^a, p. 57).
ave expressed the opinion that these cells are to be re-
fied retinular cells, it might be maintained that they are
d accessory pigment cells, such as occur in the inter-
ce of many Crustaceans. But I believe such an interpre-
cells would be erroneous, for the following reason. In
lei of the pigment cells which surround the cone (Plate VI.
) possess one, and sometimes two, well marked nucleoli,
omatine granules. In this respect they closely resemble
he proximal retinular cells (*nl. px.*), and differ consider-
e of the accessory pigment cells (*nl. h'drm.*). The nu-
named cells contain only fine granules. So far, then,
are concerned, the distal retinular cells bear a much
nce to the proximal cells than to the accessory pigment
tinula in Serolis contains, moreover, only four cells, and
differs considerably from other Isopods, where the number
ls is either six or seven. On the supposition that the
surrounding the cone in Serolis are accessory pigment
l be called upon to account for the exceptionally small
s in the retinula of this genus; whereas, if the cells
e are regarded as modified retinular cells, they may be
te for Serolis a primitive retinula composed of six cells,
cteristic of the retinulæ in other Isopods. This inter-
e condition of the retinula in Serolis is borne out by
of the retinula in Sphæroma, where, it will be remem-
ion between the condition in Serolis and that in other
stinctly indicated.

atopods, Schizopods, and Decapods, if my observations
ere are no ectodermic accessory pigment cells. Conse-
arison between these cells and what I have called the
cells cannot be drawn. In Mysis (Plate VII. Fig. 73),
Plate VIII. Fig. 94), and Palæmonetes (Plate IX. Fig.
in all other Decapods which I have examined, the resem-
the nuclei of the retinular cells and those of the pigment
round the cone is as striking as in Serolis, and suggests
hese cells from retinular cells rather than from any other
marus, the pigment cells around the cone present a con-
nterest in this connection. Each pigment cell is extended
a long fibre, which certainly reaches nearly to the base-

ment membrane, and probably passes through it in company with the fibrous ends of the retinular cells (compare Parker, '90^a, pp. 17-19). Admitting that these cells are merely modified accessory pigment cells, such a condition as this is quite unintelligible to me; but granting them to be differentiated retinular cells, their fibrous extensions can be easily explained as the rudiments of the fibrous portion of the cell with which the nerve fibre was once connected. A somewhat similar case occurs in Mysis, where the centre of each of the pigment cells which surround the cone contains a small transparent axis. This axis in every respect except that of connection with a nerve fibre corresponds to the fibrillar axes described in the functional retinular cells of this Crustacean (compare Plate VII. Figs. 77, 78, and 87). Consequently, the axis in the distal cells either represents a rudimentary nervous axis, in which case the cell containing it must be regarded as a retinular cell, or it is something for which I can suggest no explanation.

These facts lead me to conclude that the pigment cells which surround the cone in Serolis, the Stomatopods, Schizopods, and Decapods, are to be regarded as modified retinular cells, and I have therefore described them under the name of distal retinular cells, in contrast to proximal retinular cells, or those which retain their primitive position around the rhabdome. In the differentiation of a group of simple retinular cells into proximal and distal cells, the latter necessarily change their function from that of terminal nervous organs to that of screens chiefly concerned in excluding the light from the sides of the cones. Wherever the distal retinular cells occur, they afford evidence, I believe, that the structure of the ommatidium has undergone a modification from the primitive ommatidial condition.

The second method by which the structure of ommatidia may be changed, namely, the suppression of cells, is perhaps the one whose presence is most easily detected because of the frequent persistence of the partially reduced cells. These rudimentary cells can be identified most readily in the cases where they belong to groups in which the number of elements is constant for different ommatidia. I know of no evidence of suppression among the groups of cells in the corneal hypodermis or the cones. Among the retinulæ, however, it seems to be of rather common occurrence. The first indication of this process is naturally a diminution in the size of the cell to be suppressed. Such a step is perhaps shown in the retinula of Gammarus (Plate I. Fig. 6), where one of the five cells, although evidently functional, is nevertheless considerably reduced. Without much doubt, the body described in the

tea robusta represents, for reasons already stated, the
esent as a functional structure in Porcellio. In Idotea
nulæ, with very few exceptions (Plate V. Fig. 54), contain
howing no trace of the seventh cell. This condition, I
interpreted as one in which a cell has been completely
Stomatopods, Schizopods, and Decapods the retinulæ
n to contain, in addition to the nuclei of the seven func-
eighth nucleus, which may represent a rudimentary cell.
cases thus far cited, it might be maintained that what I
rudimentary cells are really cells newly acquired by the
not old cells gradually undergoing suppression. The con-
however, where the body in question apparently contains
ıld be difficult to explain on this assumption, whereas, if
a cell undergoing reduction, its condition can be easily
In Stomatopods, Schizopods, and Decapods, the con-
ımber of cells and in the position of the eighth nucleus,
ınt of protoplasm which surrounds it, and the striking
ich it has to the other retinular nuclei, are facts difficult
he assumption that it represents a newly acquired cell,
ınted for on the supposition that it is the remnant of a
ssed cell. For these reasons, I believe that the instances
ases of partial suppression, and that this must be regarded
tual means employed in the modification of ommatidia.
dia have been modified by an increase in the number
y cell division, is a proposition not easily established.
of obtaining conclusive evidence on this point can be
an example. Let it be assumed that cones composed
converted by the division of the cells into cones com-
ells. This step, even when first taken, would probably
during the embryonic growth of an animal, and there-
cones themselves had begun to be differentiated. What
happen would probably be this: the two cells, the
hich in all previous animals had given rise to two cone
this case each divide, thus producing a group of four
imately would form a cone of four segments. If we
the adult animal in which such a process had occurred
me with its immediate ancestors, the only important
would be observed would be in the number of the
one, and if the genetic relations of the two individu-
ıown, it could not be stated with certainty whether in

one case we were dealing with an animal which had lost two co or in the other, with one which had gained two; in other w would be impossible to determine which of the two conditions primitive one. The importance of embryological evidence in d ing this question must therefore be apparent. But evidence fr this source might not be conclusive. Thus in the developmen lobster I have traced in detail the steps by which the ommat formed, and although in this Crustacean the considerable nu cells in each ommatidium would warrant one in expecting some of increase by division, the division of the cells in the retina is accomplished some time before these elements show any group ommatidia. Hence, the exact method of origin of the cells of matidium cannot at present be given. I have observed that th is also true in Gammarus; cell division is completed before the grouped into ommatidia. Perhaps in the development of som Crustaceans evidence of the kind which I have sought may be o but in the few species which thus far have been studied the e has not been produced.

Although the supposition that ommatidia may increase the of their cells by the division of those which they already posses supported by any direct observations with which I am acquainte are some facts recorded which are indirectly confirmatory of it. in Phyllopods, an increase in the number of cone cells appears to pany a progressive differentiation of the retina itself. In this g I have already pointed out, the simplest condition of the retina i in Branchipus and Apus. From the retina of Apus that of the Es can be easily derived, and the retina in the Estheridæ represents dition from which the retina of the Cladocera may have arisen. this series of retinas, from Apus through the Estheridæ to the Cl is a natural one is abundantly proved by the course taken in the ment of the eye in these groups. If we regard the condition cones in these Crustaceans, we shall find that in the most p retina, that of either Branchipus or Apus, they consist of fou that in the more complex retina of the Estheridæ they are usual posed of five cells, although cones of four cells are not unfrequen rences; and finally, that in the Cladocera they are always comp five cells. Apparently in this series the development of the r paralleled by a corresponding development in the cones, where composed of four cells is ultimately converted into one with fiv Since the resemblance between any two of the cells in a cone co

s is quite as close as that between the cells in cones con-
our elements, I believe that the additional cell, which has
number of segments from four to five, has been derived by
one of the original four cone cells, and not from an extra-
urce.

tance of this kind occurs among the Isopods. The cones
it will be remembered, are usually each composed of two
ccording to Beddard's figures ('90, Plate XXXI. Figs. 1
urus, however, they occasionally consist of three segments,
aquaticus, according to Sars ('67, p. 110), although three
es in each eye are composed of only two segments each,
gularly contains three. The size of the segments in the
ffers; two are small, and together their bulk about equals
rd, and the last is approximately of the size of a segment
ther cones. If we attempt to explain the condition of the
of three segments by supposing it to have been produced
he normal pair of cone cells a single cell from some source
ommatidium, we are met with the difficulty, that what
the added cell — the larger one — resembles more closely
he other cones than do either of the two remaining cells,
latter must on this assumption represent the original seg-
wever, we imagine the small segments to have arisen by
a single larger one similar to the large one which remains
e relation of the resulting segments both in size and num-
tly natural one. This explanation, therefore, seems to me
bable than the former. For these reasons, I believe that
the number of cells in an ommatidium takes place by the
cells already forming a part of that ommatidium, rather
mportation of new elements hitherto foreign to the om-

ion which I would draw from the preceding discussion is,
at least three means of modifying the numerical formulæ
all of which involve only the cells primitively belonging
idium, and therefore do not necessitate the introduction
rom extra-ommatidial sources. They are cell differentia-
ression, and cell multiplication.

determined the means by which the cellular structure of
in living Crustaceans is modified, we are prepared to ap-
estion of the structure of the primitive ommatidium. If
own that ommatidia were modified only by increasing the

number of their elements, it would naturally follow that those composed of the fewest cells would more nearly resemble the ancestral type than those which consist of many cells. On the other hand, if the suppression of cells were the only means employed in modifying structure, the ommatidia containing the greatest number of elements would most nearly approach the primitive type. Since, as I believe, both means are employed in the Crustacea, the determination of the structure of the ancestral ommatidium is evidently a difficult problem. Perhaps the most satisfactory way of attempting its solution is to consider separately the different categories of cells which enter into the formation of an ommatidium, and, after reviewing the conditions presented by each in different Crustaceans, to determine, if possible, which of these conditions is the most primitive. The conclusions thus arrived at concerning each kind of cell will afford the necessary grounds for the construction of an hypothetical formula of the ancestral ommatidium. Although it is not necessary that this ommatidium should be represented in any living Crustacean, for the ommatidia in all these may have suffered modification, yet it is possible that a representative of it may still exist.

Turning now to the consideration of the different groups of cells, we find that the corneal hypodermis presents two conditions; one in which its cells are not regularly arranged, and another in which they are grouped in pairs, each pair lying at the distal end of an ommatidium. The latter condition is characteristic of the Decapods, Schizopods, Stomatopods, Nebaliæ, Isopods, and some Branchiopods; the former, so far as is known, occurs in the Amphipods, the Branchiura, and in some Branchiopods (Limnadia and some species of Branchipus). In view of the fact that the corneal hypodermis is a part of the retina which retains the function of the general hypodermis but slightly modified, and that in the latter the cells do not present a regular arrangement, it is probable that a corneal hypodermis in which the cells are not regularly arranged is of a more primitive character than one in which they are definitely grouped.

The number of cells in the individual cones of Crustaceans varies from two to five. Cones composed of two cells occur in Eucopepoda, Amphipods, Isopods, and Schizopods; cones of three cells are present only exceptionally in Isopods; cones of four cells are found in the Decapods, Stomatopods, Nebaliæ, Branchiura, and some Branchiopods; cones of five cells characterize the Cladocera and some Branchiopods. I have already given reasons for regarding the cones composed of three cells as having been derived from those containing two, and cones com-

cells from those possessing four. Since there is no evidence
e cells in any of the cones composed of two segments, I am
at cones with four cells are derived from those with two cells,
everse. On these grounds, I conclude that the most primi-
one in living Crustacea is that consisting of two cells.

lar cells in Crustaceans are subject to considerable varia-
ave previously shown, an ommatidium may contain one or
When there is only one kind, all the cells are grouped
abdome, and are known simply as retinular cells. When
kinds, one occupies a position around the rhabdome, and
und the cone; the former I have called proximal retinular
ter distal retinular cells. Proximal and distal retinular
n Serolis, the Stomatopods, Schizopods, and Decapods;
lar cells apparently characterize the ommatidia of all other
I have already presented reasons for considering the
ar cells as modified simple retinular cells, which, in the
the cone from the rhabdome by the elongation of the
have lost their connection with the nervous element, but
their place next the dioptric one. A group of retinular
this differentiation has occurred is not so primitive in its
refore, as one in which all the retinular cells retain their
ion around the rhabdome, as in the groups of Crustacea
simple retinular cells.

r of simple retinular cells in Crustacean ommatidia varies
seven. In Nebalia, and some Isopods, the retinula con-
lls; in other Isopods it is composed of six cells, and in
pods, the Cladocera, some Copepods, and Amphipods it
e cells. It is difficult to state which of these numbers
primitive condition. In the Isopods, as I have previ-
ed (pp. 86 and 87), there is considerable evidence to
etinula composed of six cells has been produced from one
ven by the suppression of one cell. Possibly in this way
ith five cells was derived from that with six, but I know
tions which favor this supposition.

nount of indirect evidence on this question is to be ob-
the other structural peculiarities of the ommatidia con-
ulæ with five, six, or seven cells. These retinulæ occur
with two kinds of rhabdomes, — one in which the rhab-
ents are easily distinguishable, and the other from which
rently absent. Of these two kinds, the one in which the

segments persist is evidently more primitive than the one in which their outlines are obliterated.

Probably in Nebalia, in which the retinula is composed of seven cells, and certainly in Idotea, where it consists of six, the rhabdome shows no indication of being composed of rhabdomeres, but in Porcellio the seven retinular cells surround a rhabdome composed of a corresponding number of rhabdomeric segments. In Branchipus, the retinula consists of five cells, but the rhabdome is apparently not composed of separable rhabdomeres, whereas in Pontella, Argulus, Gammarus, Talorchestia, Hyperia, and Phronima the five retinular cells are each represented by a rhabdomere. The more frequent occurrence of a primitive condition of rhabdome with the retinula having five cells than with that having seven, favors indirectly the idea that the retinula with the smaller number of cells is the more primitive of the two. The types of cones associated with the two kinds of retinulæ offer almost no evidence on the question in hand. Thus, a retinula of seven cells is associated with a cone of four cells in Nebalia, and with one of two cells in Porcellio, and a retinula of five cells is combined with a cone of four cells in Branchipus and Argulus, and with one of two cells in Amphipods. The relation of the two kinds of retinulæ to the corneal hypodermis affords some slight evidence in support of the opinion that the retinula of five cells represents the more primitive type; for although the differentiated type of corneal hypodermis — the one in which the cells are regularly arranged — may occur with either type of retinula, the undifferentiated hypodermis — in which the cells are not regularly grouped — is known to be associated only with retinulæ containing five cells (some Branchiopods, Argulus, and Amphipods). The evidence drawn from these various sources is obviously very slight; but such as it is, it indicates that the retinula with five cells, rather than that with a greater number, represents the more primitive condition. This conclusion receives some additional support from the fact that the retinula composed of five cells characterizes the ommatidia in a number of not otherwise very closely related Crustaceans (Pontella, Argulus, the Branchiopods, and Amphipods), whereas the type possessing seven cells occurs only among certain Isopods and in the Nebaliæ. I believe, therefore, that all the evidence at present deducible from the condition of the simpler retinulæ indicates that the one which contains five cells is more primitive than that composed of six or seven cells.

In the present argument I have purposely omitted any mention of the condition of the retinula in the Corycæidæ, those Copepods in which the

eral eyes present a highly modified condition. I have done this be-
se I believe that the lateral eyes in many Copepods are degenerate,
d that therefore the evidence to be drawn from them cannot be as
stworthy as that from other sources. That the lateral eyes in Cope-
ds are degenerate, is shown from the fact that in many members of
e group the eyes are entirely absent, and that in those in which they
occur, their structure is subject to considerable variation. Thus in
ntella the retina contains, besides one group of five retinular cells, three
lated nervous cells, whereas in Sapphirina there is a group of three
inular cells, and at least one isolated nervous cell. In Pontella, Sap-
irina, Corycæus, and Copilia each retina is provided with a single lens,
t in Irenæus, according to Claus ('63, Taf. II. Fig. 1), there are two
ses in each eye. These variations, including the total disappearance
the organ in some members of the group, lead me to believe that the
eral eyes in the Copepods are degenerated, and therefore are organs
which the suppression of cells may have reduced them to even a
mpler condition than that presented by the ancestral ommatidium.

The conclusion which I draw from the preceding argument is, that the
pe from which the ommatidia in all living Crustaceans are probably
rived would exhibit the following structures: a corneal hypodermis in
ich the cells are not regularly arranged, and consequently an un-
etted corneal cuticula; a cone composed of two cells; a retinula com-
sed of five retinular cells and having a rhabdome which consists of
e rhabdomeres. The retina of the primitive eye, a simple thickening
the superficial ectoderm, would be composed of ommatidia of this
pe arranged upon the hexagonal plan. None of the Crustaceans
th which I am acquainted possess an eye of exactly this structure.
e one in which this condition is most nearly represented is perhaps
mmarus. In this animal all the requirements of the hypothetical
e are fulfilled, except that the form of the retina as a whole is some-
at disturbed by the separation of the corneal hypodermis from the
yer of the cones and retinulæ by a corneo-conal membrane, and by the
rtially disguised condition of the basement membrane.

If my conclusions be correct concerning the structure of the primitive
matidium and the means by which it has been modified, it follows
at the principal types of ommatidia have been produced mainly by
creasing the number of cells in the primitive type, and that, of the
ree means of modifying the structure of ommatidia, cell division has
en the most influential.

Although the hypothetical ommatidium which has been described in the preceding paragraphs has been spoken of as ancestral, it is not to be supposed that the condition which it presents must be regarded as necessarily its simplest form. I feel tolerably confident, however, that the primitive ommatidium must have been at least as simple as I have assumed it to be. Possibly its retinula may have been composed of less than five cells, as is that seen in some Copepods; although, as I have previously remarked, the condition of the lateral eyes in these Crustaceans is probably influenced by degeneration, and therefore may not represent a primitive stage. What might be regarded, however, as a more primitive form of ommatidium than that which I have described, may be seen in the eye of the Chætopod Nais (Carrière, '85, pp. 28, 29). In this worm the eye lies in the hypodermis on the side of the head, and consists of a few relatively large transparent cells, the proximal faces of which are in part covered by pigment cells. It is probable that the transparent cells are merely dioptric in function, and that the pigment cells are nervous. The transparent cells may therefore be looked upon as the forerunners of cone cells, and the pigment cells at their bases as retinular cells not yet differentiated into a retinula. It is not difficult to imagine the origin of an ommatidium from a single one of the transparent cells and its accompanying pigment cells, and, by an increase in the number of such groups, the production of a retina like that of the compound eye of Arthropods.

This view of the origin of the ommatidia in Arthropods is irreconcilable with that recently advanced by Watase ('90), according to whom each ommatidium is to be regarded as a pit formed by an involution of the hypodermis. The supposed cavity of this pit occupies nearly the whole length of the axial portion of the ommatidium, and is filled by the secretions of the cells constituting its wall. The secretion in the deeper part of the pit forms the rhabdome; that which is produced nearer its mouth, the cone. During the formation of the pit, the hypodermal cells are believed to retain such mutual relations that their morphologically distal ends lie next its cavity; hence the secretions produced by these ends, the rhabdome and cone, are to be regarded as modifications of the chitinous cuticula of the outer surface of the body.

Ingenious as this theory is, I have not been able to convince myself of its tenability. It may be urged against the assumption that the retinular cells occupy a proximal position and the cone cells a distal one on the wall of a hypodermal pocket, that in Gammarus the retinular cells extend from the distal to the proximal face of the retina, and that in Homarus the cone cells have a corresponding extent; these conditions show that is possible to interpret the cells in an ommatidium as elements in a ckened epithelium, all of which originally extended from one face of layer to the other, and the grouping of which is not even now in- fered with by any process of involution. But granting that the ret- l cells are thus arranged, it must be admitted that the surface on ich the rhabdomeres are produced corresponds to the *sides* of the cells her than to their *distal ends*. This interpretation of the position of rhabdome is not, so far as I am aware, contrary to any well estab- ed facts, and indeed it is rather more in accordance with the condi- n seen in the eyes of some Arthropods than that implied in Watase's eory. Thus, in the lateral eyes of scorpions the retinal cells are ar- ged as in an ordinary epithelium, and the lateral wall of each cell is part occupied by a rhabdomere. In this instance, then, it must be mitted either that the rhabdomeres are produced on the *sides* of the inal cells, or that each cell has independently rotated upon itself, so to bring its morphologically distal end into a position corresponding the side of an ordinary epithelial cell. But there is neither direct dence to show that this rotation of single cells has occurred, nor, in s case, can there be any motive assumed which might have induced rotation of single elements. I therefore believe that in the lateral es of scorpions the rhabdomes are on the sides of the retinal cells in strictest morphological sense; and if they can occur in this position the eyes of scorpions, I can see no reason why they might not occur similar positions on the retinal cells of compound eyes. Hence it ms to me as reasonable to interpret the retina in compound eyes as a er of modified epithelium unaffected by involutions, as it is to con- er it a layer in which each ommatidium represents an infolding.

When, moreover, an attempt is made to show how a particular omma- ium has arisen by involution, some difficulties are encountered. Thus Gammarus, in which the ommatidium is of a primitive type, each om- tidial pocket would involve seven cells, two of which, the cone cells, st be imagined as forming the neck of the involution, while the re- ining five, the retinular cells, would constitute the deeper portion of pocket. The mechanical difficulty which would accompany the forma- n of an involution involving so small a number of cells must be obvi- s, and offers, I believe, an obstacle to the successful operation of the ocess assumed in Watase's theory.

The one instance in which Watase has described an actual involution form the eyes in Arthropods is the lateral eye of Limulus. These eyes nsist of a cluster of hypodermal pits, over each of which there is a cuticular lens. Although there cannot be the least doubt that in this case each pit is a hypodermal involution, the belief that each one is homologous with an ommatidium is by no means so well founded. In structure the wall of the pit differs considerably from that of an ommatidium; it contains no cells which can be definitely denominated, either as cone cells or as cells of the corneal hypodermis, and it does contain a large ganglionic cell, which is only questionably homologous with any element in an ommatidium. In most respects in which these pits differ from ommatidia, they resemble simple eyes, and I therefore regard them as such, rather than as representatives of an early condition in the formation of an ommatidium.

When to the objections raised in the preceding paragraphs the statement is added, that in both Homarus and Gammarus — representatives of the extremes of organization — the ommatidia are developed without showing any trace of infolding, Watase's theory of the formation of ommatidia by means of involutions appears in a still less favorable light. I therefore regard ommatidia, not as the result of involutions, but as differentiated clusters of cells in a continuous unfolded epithelium.

I have not observed anything that would lead to the conclusion recently expressed by Patten ('90), that an ommatidium is a hair-bearing sense bud. I believe, on the contrary, that they have had a very different origin.

In conclusion, I may add, that if my idea of the origin of ommatidia be correct, it supports Grenacher's opinion, that compound eyes are not derived directly from aggregations of simple eyes, but from groups of optic organs which were even more primitive in their structure than simple eyes. Possibly such primitive organs were the antecedents of both the compound and simple eyes of Arthropods, as Grenacher suggests; but possibly the two kinds of eyes may have had totally different origins.

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EXPLANATION OF FIGURES.

All the drawings were made with the aid of an Abbé camera. Unless otherwise stated, the specimens from which the drawings were made were stained in Czokor's alum-cochineal and mounted in benzol-balsam. The reagent used in depigmenting sections was an aqueous solution of potassic hydrate ½%.

ABBREVIATIONS.

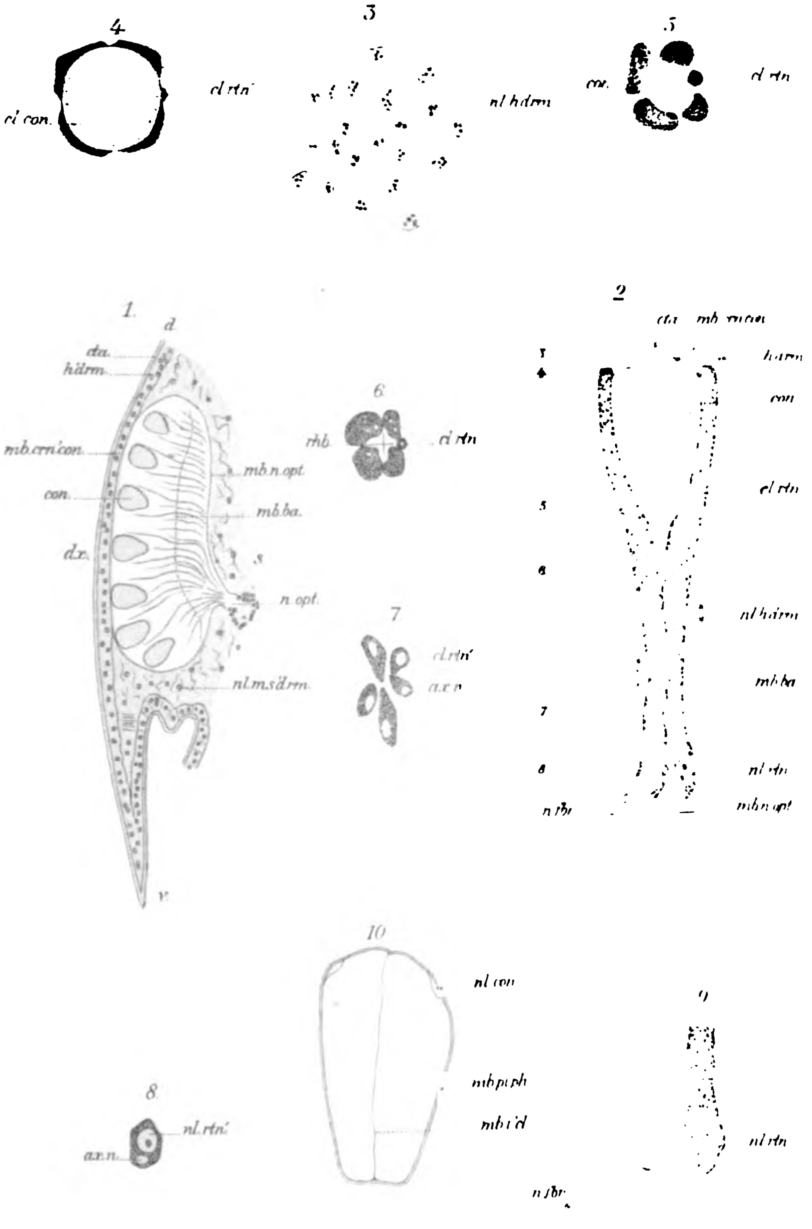
a.	Anterior.
ax. n.	Axis of nerve fibrillæ.
brs. oc.	Optic pocket.
cl. con.	Cone cell.
cl. crn.	Cell of corneal hypodermis.
cl. dst.	Distal retinular cell.
cl. hyl.	Hyaline cell.
cl. ms'drm.	Mesodermic cell.
cl. px.	Proximal retinular cell.
cl. rtn.'	Retinular cell.
cl. rud.	Rudimentary retinular cell.
cnch.	Shell.
cœl.	Body cavity.
con.	Cone.
cp. sng.	Blood corpuscle.
crn.	Corneal cuticula.
cta.	Cuticula.
d.	Dorsal.
dsc.	Sucking disk.
dx.	Right.
gn. opt.	Optic ganglion.
h'drm.	Hypodermis.
hp.	Liver.
in.	Intestine.
lns.	Lens.
mb. ba.	Basement membrane.
mb. crn.	Corneal membrane.
mb. crn'con.	Corneo-conal membrane.
mb. i'cl.	Intercellular membrane.
mb. n. opt.	Membrane of optic nerve.
mb. pi'ph.	Peripheral membrane.
mb. pr'con.	Preconal membrane.
mu.	Muscle.
n. fbr.	Nerve fibre.
nl. con.	Nucleus of cone cell.
nl. crn.	Nucleus of cell in corneal l podermis.
nl. dst.	Nucleus of distal retinular c
nl. h'drm.	Nucleus of hypodermal cel
nl. hyl.	Nucleus of hyaline cell.
nl. ms'drm.	Nucleus of mesodermic cel
nl. px.	Nucleus of proximal retinu cell.
nl. rtn.'	Nucleus of retinular cell.
n. opt.	Optic nerve.
oc.	Eye.
omm.'	Ommateum.
p.	Posterior.
po. brs.	Pore of optic pocket.
r.	Retina.
rhb.	Rhabdome.
rhb'm.	Rhabdomere.
rtn.'	Retinula.
s.	Left.
v.	Ventral.
va. sng.	Blood-vessel.

Such other abbreviations as have been used are explained in the description the figures with which they occur.

PLATE I.

Gammarus.

Fig. 1. A section of the right eye in a plane transverse to the chief axis of
body and through the central part of the retina. × 115.
" 2. A section lengthwise of an ommatidium. The numbers at the le
the figure correspond to the numbers of the six following fig
of transverse sections, and mark the levels at which the latter
taken. × 475.
" 3. A transverse section in the plane of the corneal hypodermis. × 47
" 4. A transverse section through the distal ends of the retinular cells
cone. × 475.
" 5. A transverse section through the proximal portion of the cone
through the adjoining retinular cells. × 475.
" 6. A transverse section through the retinula in the region of the rhabd
× 475.
" 7. A transverse section through the retinular cells somewhat proxim
the basement membrane. × 475.
" 8. A transverse section through a single retinular cell in the region o
nucleus. × 475.
" 9. The proximal portion of a retinular cell viewed from the side. (Com
Fig. 2.) Isolated in Müller's fluid. Not stained. × 475.
" 10. A cone isolated in Müller's fluid and viewed from the side. Not stai
× 475.



G.H.P. del.

GAMMARUS.

PLATE II.

Argulus.

(Figs. 11–17.)

Fig. 11. A section in a plane transverse to the chief axis of the body and thr
the right eye. Depigmented. × 140.

" 12. A longitudinal section of an ommatidium. × 475.

" 18. A longitudinal section of an ommatidium which had been depigmen
The numbers at the left of the figure correspond to the num
of the four following figures of transverse sections, and mark
levels at which the latter were made. × 475.

" 14. A transverse section through the distal end of a cone and the surro
ing pigment cells. × 475.

" 15. A transverse section through the proximal portion of a group of
cone cells. The intercellular membranes of the cells present
thickened regions. × 475.

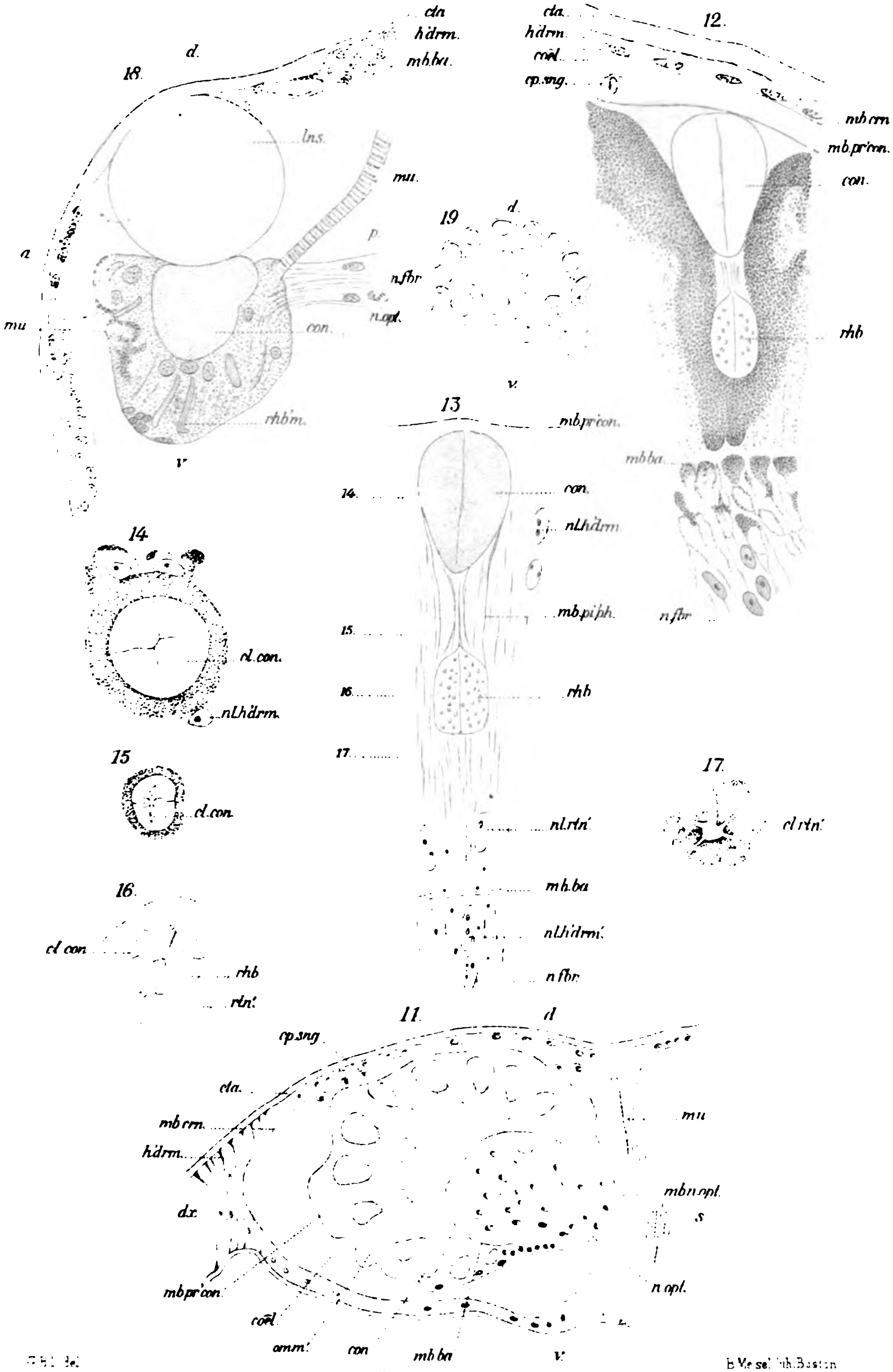
" 16. A transverse section through the rhabdome. Depigmented × 47

" 17. A transverse section through the retinula somewhat proximal t
rhabdome. × 475.

Pontella.

Fig. 18. The left lateral eye seen from the left side. The section is an o
one; its plane is very nearly parallel to the sagittal plane o
body. Depigmented in alcohol (see p. 78). × 275.

" 19. A transverse section of the optic nerve from a region immediately
rior to the retina. The sagittal plane divides the nerve into
metrical halves; the fibres in each half belong exclusively t
lateral eye of the corresponding side. × 400.



G.H.P. del.

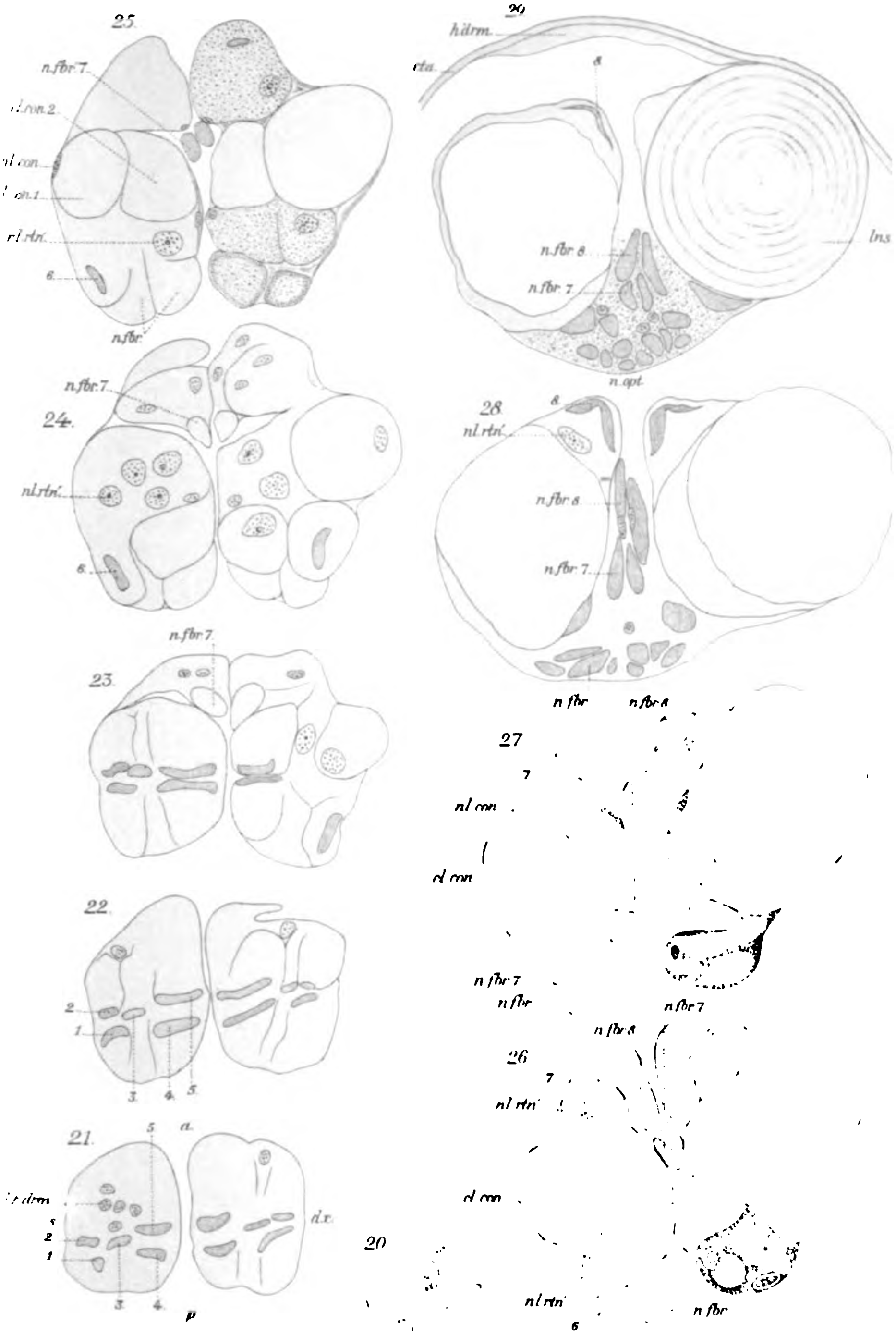
B. Meisel lith. Boston

COPEPODA.

PLATE III.

Pontella.

Figs. 20–29. A complete series of ten consecutive sections through the right
left retinas in planes parallel to the horizontal plane of the ani
The sections are viewed from their dorsal faces. Figure 20 repres
the most ventral section; Figure 29, the most dorsal. The plan
Figure 25 is approximately indicated by the incomplete dotted
mu. con. in Figure 18 (Plate II.). In the sections on the present p
the different bodies in the left retina have been designated by appro
ate letters and figures. The eight rhabdomeres have been indic
simply by numbers; the same number always refers to the s
rhabdomere. For the sake of distinction, the two cone cells h
been marked *cl. con. 1* and *cl. con. 2*. Some of the nerve fil
(*n. fbr. 7* and *n. fbr. 8*) have been numbered in reference to the
ticular rhabdomeres with which they are associated. × 400.



G.H.P. del.

PONTELLA.

B. Meisel lith. Boston

PLATE IV.

Branchipus.

(Figs. 30–32.)

Fig. 30. A longitudinal section of an ommatidium. × 400
" 31. A transverse section through the distal end of four cones. × 400.
" 32. A transverse section through the middle portion of a retinula. × 4

Limnadia.

(Figs. 33–39.)

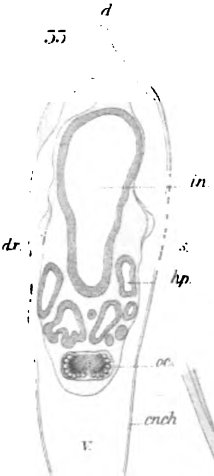
Fig. 33. A section through the anterior part of the body, including the eye
plane transverse to the chief axis. × 25.
" 34. An enlarged portion of a section from the same series as that from
Figure 33 was drawn, but in a position slightly anterior to th
ter. × 115.
" 35. A section through the eye cut in the sagittal plane of the animal.
pigmented. × 90.
" 36. A lateral view of an ommatidium. The numbers at the left o
figure correspond to the numbers of the three following fi
of transverse sections, and mark the levels at which the latter
taken. × 475.
" 37. A transverse section through the corneal hypodermis and distal en
the cones. × 475.
" 38. A transverse section through four cones at the level where the
thickest. × 475.
" 39. A transverse section through the central portion of four retinulæ. ×

Evadne.

(Figs. 40–45.)

Fig. 40. An optical section through the eye and adjoining structures in a
approximately parallel to the sagittal plane of the body, but
somewhat to the right of it. × 140.
" 41. A transverse section through the distal ends of the cones. × 475.
" 42. A transverse section through the proximal end of a cone. × 475.
" 43. A transverse section through the distal ends of three groups of reti
cells. In each group the corresponding cells have been desig
by the same number. × 475.
" 44. A transverse section through the central part of four rhabdomes. ×
" 45. A transverse section through a retinula. Depigmented. Kleinen
alum-hæmatoxylin. × 475.

33.



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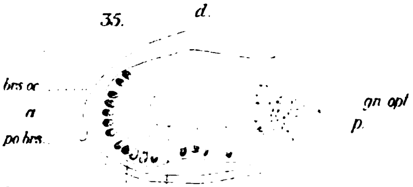

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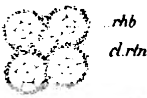

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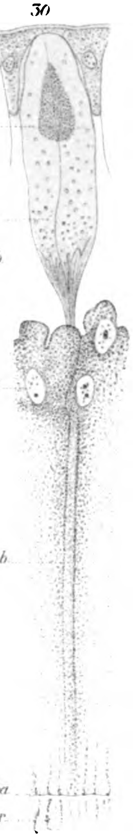

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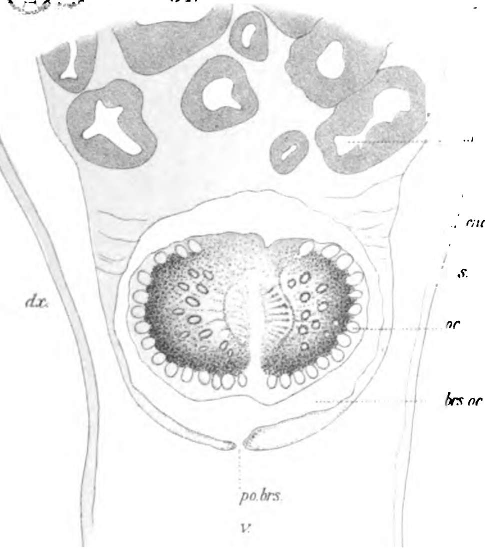

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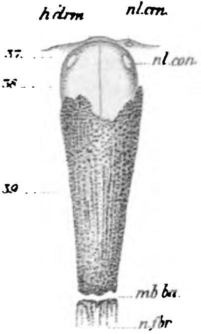

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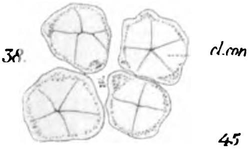

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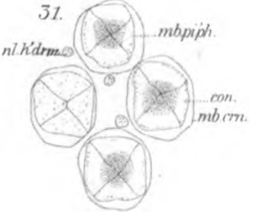

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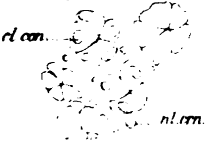

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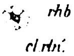

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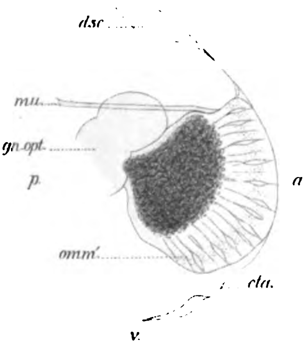

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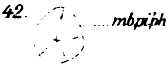

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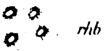

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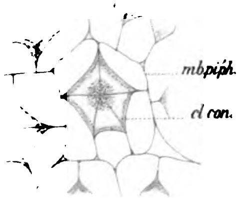

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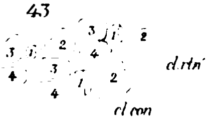


G.H.P. del.

PHYLLOPODA.

B. Meisel lith. Boston.

PLATE V.

Porcellio.

Fig. 46. A transverse section through a retinula in a plane slightly distal to basement membrane. The single, light, central spot represents proximal end of the rhabdome. × 475.

Idotea robusta, Kroyer.

(Figs. 47, 48.)

Fig. 47. A transverse section through the distal end of a retinula. The bod one of which is marked *x*, are spheres of coagulated material wh occur in the interommatidial spaces, and which have been brou into prominence by the action of the hardening reagent. × 475.

" 48. A transverse section through three ommatidia in the region of th rhabdomes. × 475.

Idotea irrorata, M. Edws.

(Figs. 49–57.)

Fig. 49. The anterior face of a section transverse to the chief axis of the bo and passing through the eye on the right side of the head. × 14

" 50. A longitudinal section of an ommatidium. The numbers at the lef the figure correspond to the numbers of the following six figu of transverse sections and mark the levels at which the latter w taken. × 475.

" 51. A transverse section through the distal ends of the cones. × 475.

" 52. A transverse section through the middle region of a cone. × 475.

" 53. A transverse section through the middle of a retinula. Near the cen of each cell can be seen a small axis of nerve fibrillæ. × 475.

" 54. A transverse section through a retinula composed of seven cells inst of six. This section was cut approximately at the same level as t shown in the preceding figure. × 475.

" 55. A transverse section through a retinula near its proximal end. Ea fibrillar axis is much larger at this plane than in that shown in F ure 53. × 475.

" 56. A transverse section of several groups of retinular cells immediat proximal to the basement membrane. × 475.

" 57. A transverse section of four retinular cells at the level in which th nuclei occur. The axis of nerve fibrillæ in the plane of this sect and in that of the preceding one (Fig. 56) are smaller than th are at the base of the retina (compare Fig. 55).

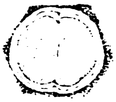
Sphæroma.

(Figs. 58, 59.)

Fig. 58. A transverse section of a retinula at a level slightly distal to the ba ment membrane. × 475.

" 59. A transverse section of the fibrous ends of the cells from a single tinula. The plane of section is slightly proximal to the basem membrane. The only indication of an axis of nerve fibrillæ is more transparent condition of the central part of the cells, due to partial absence of pigment granules. × 475.

52.



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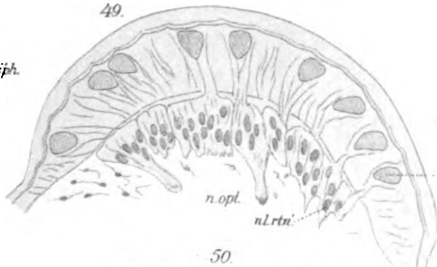

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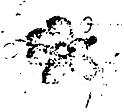

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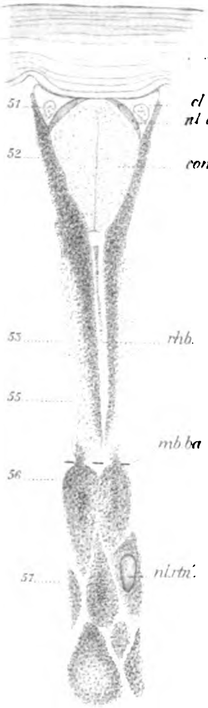

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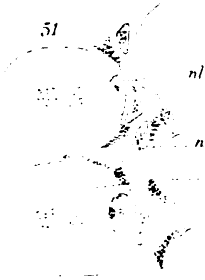

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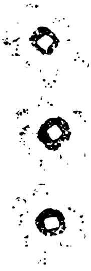

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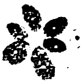

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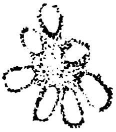

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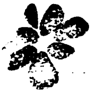

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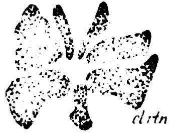

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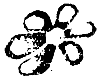

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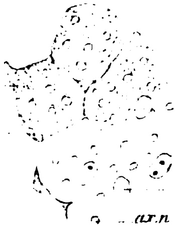

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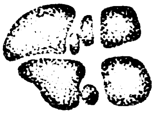


G.H.P. del.

ISOPODA.

F. Meisel lith Boston

PLATE VI.

Serolis.

Figures 60 to 64 inclusive represent the structure of the ommatidium i adult. Figures 65 to 72 are drawn from sections of ommatidia in we vanced embryos. All figures are magnified 475 diameters.

Fig. 60. A tangential section through the most distal portion of the retina. section includes a portion of a cone and the tissue lying betwe and two adjoining cones.

" 61. A transverse section of a retinula in the region of its rhabdome. arrangement of the pigment granules and nerve fibrillæ is indi in only one of the four cells. Of the two lines which appe separate the cone cells (*cl. con.*) from the rhabdomere (*rhb'm.*) one nearer the axis of the ommatidium is the real line of se tion; the other lies within the substance of the rhabdomere (compare p. 92).

" 62. A transverse section through a retinula proximal to the rhabdome in the region of the hyaline cell. As in Figure 61, the pig granules are drawn in only one of the retinular cells.

" 63. A transverse section through a single retinular cell in the region nucleus. The axis of nerve fibrillæ is represented by several axes in the substance of the cell at one side of the nucleus.

" 64. A transverse section of the fibrous ends of the cells of one retinu their passage through the aperture in the basement memb Each cell shows a well marked fibrillar axis, the centre of whi often occupied by a core of pigment. The basement membra viewed from its distal face. The irregularly oval body in the left-hand corner of the figure is probably a nucleus. It lies o proximal face of the membrane through which it is seen.

" 65. A longitudinal section through the ommatidium of an advanced em The numbers at the left of the figure correspond to the numbe the six following figures of transverse sections, and indicat levels at which the latter were taken. Figure 68 represents tion so nearly in the same plane as that shown in Figure 67 th number has been omitted.

" 66. A transverse section at the level of the corneal hypodermis.

" 67. A transverse section through the distal end of a cone.

" 68. A transverse section made in a plane only slightly proximal to shown in Figure 67.

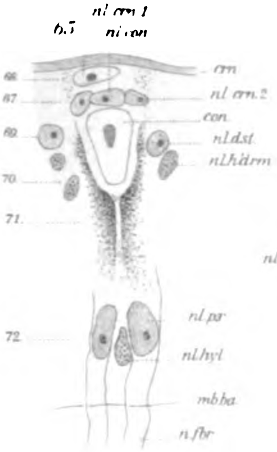
" 69. A transverse section through the region of the distal retinular nucle

" 70. A transverse section through the proximal ends of the cones.

" 71. A transverse section through the retinula in the region of the rhabd

" 72. A transverse section at the level of the proximal retinular nuclei.

6.5



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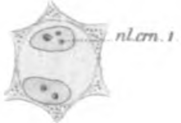

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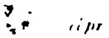

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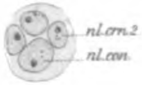

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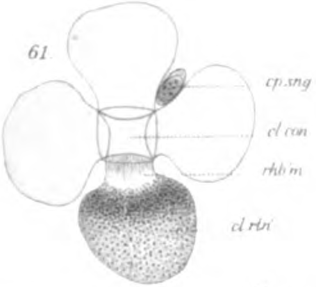

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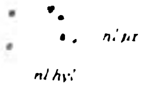

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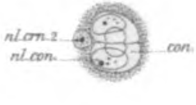

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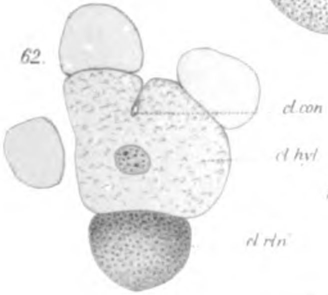

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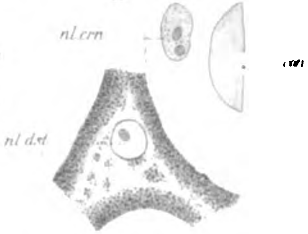

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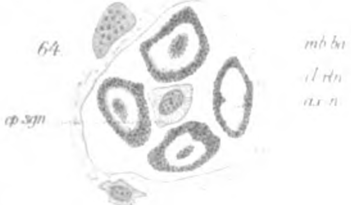

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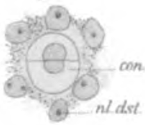

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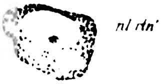


H P del.

SEROLIS

PLATE VII.

Mysis.

Fig. 73. A longitudinal section of an ommatidium. The numbers at the l
the figure indicate the levels at which the sections for Figures
were taken. × 475.

“ 74. The distal face of a corneal facet, cleaned in potash and examin
water. × 475.

“ 75. A transverse section of three ommatidia in the plane of the cornea
podermis. × 475.

“ 76. A transverse section through the distal end of a cone. × 475.

“ 77. A transverse section through the proximal end of a cone and the ad
ing distal retinular cells. × 475.

“ 78. A transverse section similar to that shown in the preceding fi
except that it is depigmented and stained in Kleinenberg's
hæmatoxylin. × 475.

Figures 79 to 82 inclusive represent consecutive transverse sections through
region of the proximal retinular nuclei of four adjacent ommatidia.
centre of each ommatidium is indicated by the group of cone cells (*cl.*
and the corresponding ommatidia in different sections are designated by
same Roman numeral. The nuclei around ommatidium II. have been n
bered in Figures 79–81. Figure 79 represents the most distal section
Figure 82 the most proximal one of the series.

Fig. 79. The bodies marked *x* and *y* are portions of nuclei the rest of which
correspondingly marked in Figure 80. × 475.

“ 83. A transverse section of the four fibres at the distal end of the rod (
pare p. 102). Depigmented, and stained in Kleinenberg's alum-h
atoxylin. × 615.

“ 84. A transverse section of the rod at a slightly more proximal level
that shown in Figure 83. Depigmented, and stained in Kleinenb
alum-hæmatoxylin. × 615.

“ 85. A transverse section of the retinula somewhat distal to the distal
of the rhabdome (compare Fig. 90). Depigmented, and staine
Kleinenberg's alum-hæmatoxylin. × 615.

“ 86. A transverse section from the region between the distal end of the r
dome and the proximal end of the rod (compare 86 in Fig. 90).
pigmented, and stained in Kleinenberg's alum-hæmatoxylin. ×

“ 87. A transverse section through the rhabdome and surrounding reti
cells. × 615.

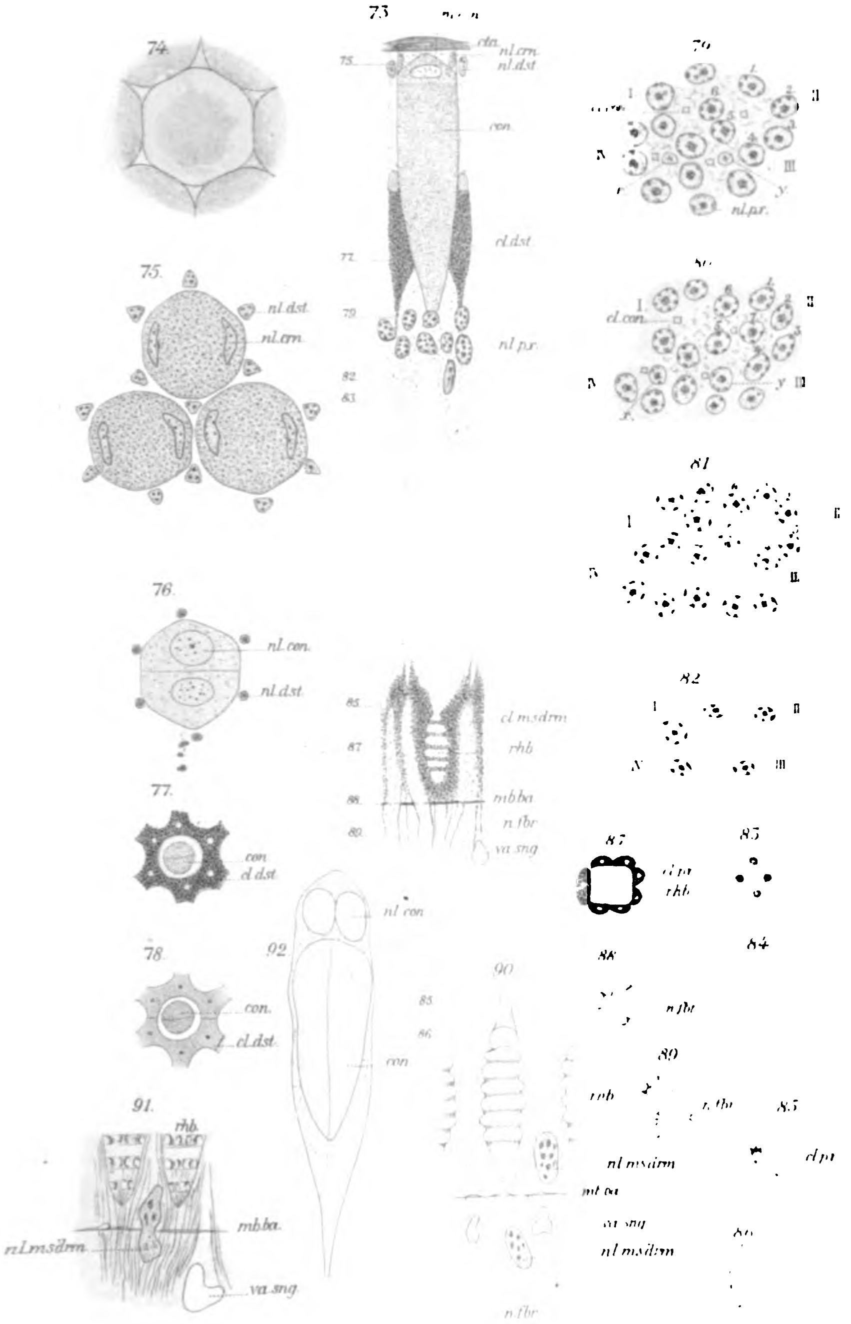
“ 88. A transverse section, at the level of the basement membrane, thr
the nerve fibres from a single retinula. Depigmented, and st
in Weigert's hæmatoxylin. × 615.

“ 89. A transverse section through the fibres of the optic nerve at a level
way between retina and optic ganglion. Preparation as in Fi
88. × 615.

“ 90. A longitudinal section through the basal portion of one and parts of
adjoining ommatidia. Depigmented, and stained in Kleinenb
alum-hæmatoxylin. × 615.

“ 91. A section cut in the same plane as that shown in the previous fi
but including only the proximal ends of two rhabdomes. Pre
tion as in Figure 90. × 615.

“ 92. A cone viewed from the side. Isolated in Müller's fluid and studi
water. × 475.



G.H.P. del.

MYSIS.

PLATE VIII.

Gonodactylus.

Fig. 93. Part of a tangential section through a superficial portion of the re The extreme edges of the section both right and left are immedia beneath the corneal cuticula; the central portion is farthest from cuticula. At the right of the middle line are seen the ends of larger ommatidia; at the left, those of the smaller. × 275.

" 94. A longitudinal section of a large ommatidium. The numbers at the of the figure correspond to the numbers of six figures of transv sections (Figs. 96–101), and mark the levels at which the latter made. Depigmented. × 275.

" 95. A longitudinal section of a small ommatidium containing its nat pigment. × 275.

" 96. A transverse section through the cells of the corneal hypodermis and distal end of the cone in a large ommatidium. × 275.

" 97. A transverse section through the distal part of a cone in a large om tidium. × 275.

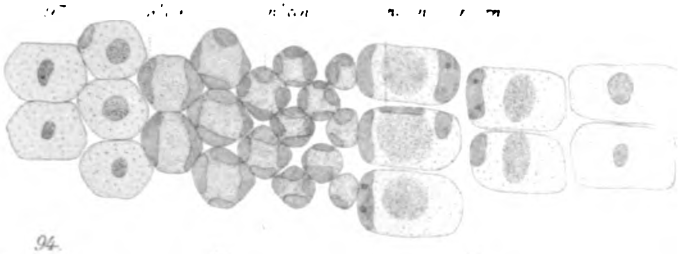
" 98. A transverse section through the middle of a cone from a large om tidium. × 275.

" 99. A tranverse section through a number of cones at the level of the di retinular nuclei in the large ommatidia. × 275.

" 100. A transverse section through six retinulæ of the large ommatidi the region of the proximal nuclei. Each retinula is numbered. plane of this section is slightly oblique, so that retinula 1 is cut relatively higher level than any of the others, and retinula 6 at lowest level. × 475.

" 101. A transverse section of a retinula from one of the larger ommatidia, plane not far from the basement membrane. Depigmented. ×

" 102. A transverse section of a retinula from one of the smaller ommatidia in a plane nearly corresponding to that of Figure 101. × 475.



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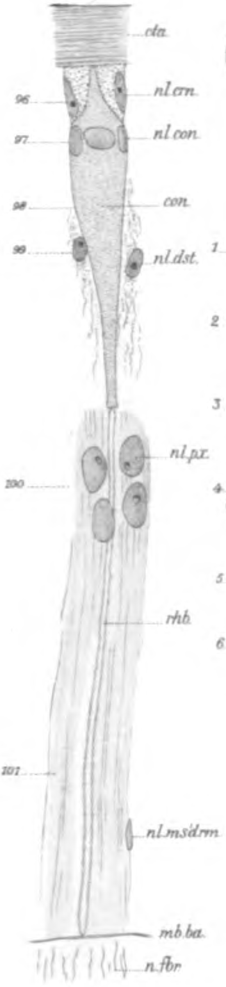

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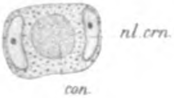

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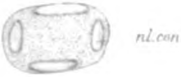

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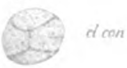

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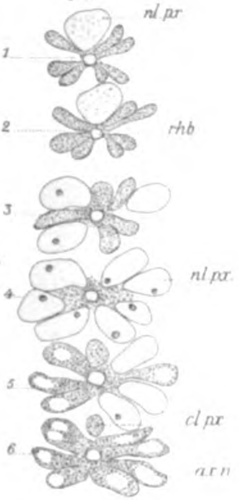

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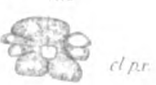

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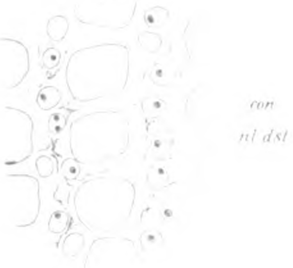


G.H.P. del.

GONODACTYLUS

PLATE IX.

Palæmonetes.

In all Figures on this plate the magnification is 475 diameters.

Fig. 108. A longitudinal section of an ommatidium. The numbers at the lef
the figure correspond to the numbers of nine of the following
ures of transverse sections, and mark the levels at which the la
were taken.

" 104. A longitudinal section of an ommatidium which has been depigmen
The bodies marked *x* resulted from the action of the depigmen
reagent.

" 105. A facet from the corneal cuticula; cleaned in strong potassic hydr
and examined from its distal side in water.

" 106. A transverse section through the region of the corneal hypodermis.

" 107. A transverse section through the distal end of a cone in the regio
the nuclei of the cone cells.

" 108. A transverse section through the middle of a cone.

" 109. A transverse section through parts of four ommatidia in the regio
the distal retinular nuclei.

Figures 110–112 represent three successive transverse sections, each thro
five ommatidia, in the region of their proximal retinular nuclei. Only
outlines of the nuclei and the five groups of cone cells (*cl. con.*) are dra
The nuclei in each ommatidium are numbered from 1 to 7, and as their
of arrangement is the same in the different ommatidia, corresponding nu
have been designated by the same number. In some cases the nuclei
cut in two, and consequently appear in two adjoining sections. In
cases the two parts have been marked with the same number. Figure
is the most distal of the series; Figure 112, the most proximal.

Fig. 113. A transverse section of the retinula near the distal end of the rhabdo
Depigmented.

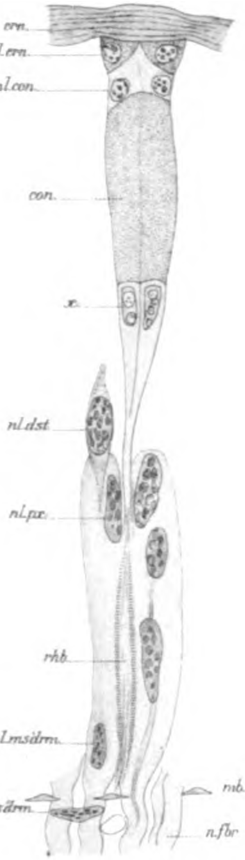
" 114. A transverse section of four retinulæ at the level of the eighth retin
nucleus.

" 115. A transverse section through four retinulæ in the region of the acces
pigment cells; viewed by *reflected* light. The retinulæ appea
dark masses embedded in a whitish field composed for the most
of the substance of the accessory pigment cells.

" 116. A transverse section through a retinula at about the same level as
shown in Figure 115. Depigmented.

" 117. A transverse section through the optic nerve fibres at a level slig
proximal to the basement membrane. Depigmented.

104



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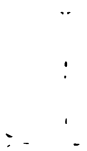

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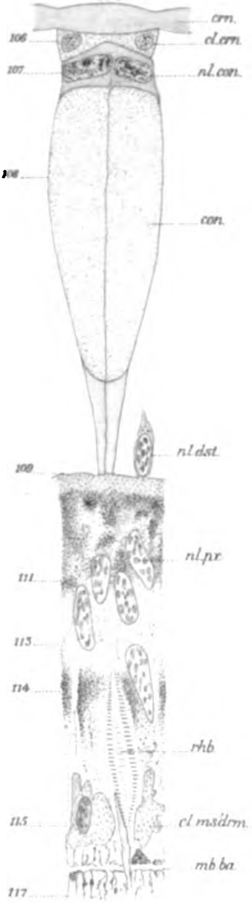

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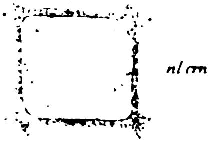

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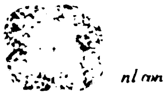

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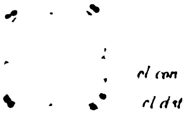

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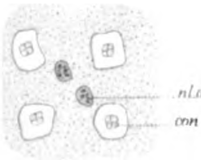

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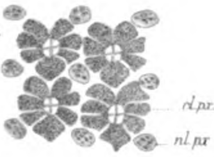

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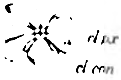

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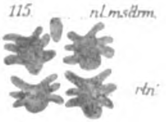

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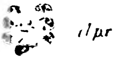

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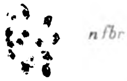

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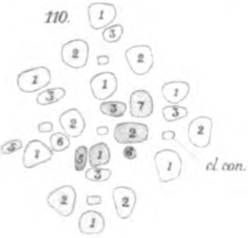

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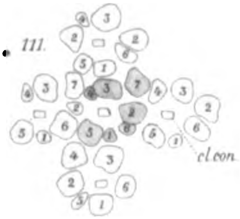

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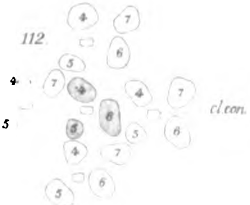


G.H.P del.

PALÆMONETES.

E. Meisel lith. Boston.

PLATE X.

In all Figures on this plate the magnification is 475 diameters.

Cambarus.

**Figures 118–122 represent a series of five successive transverse sections througl
and parts of four adjoining ommatidia in the region of their prox
retinular nuclei. Figure 118 represents the most distal sectio
the series; Figure 122, the most proximal. In these figures,
the outlines of the nuclei and the groups of cone cells are drawn**

Crangon.

**Fig. 123. A transverse section through a number of ommatidia in the regio
their distal retinular nuclei.**

Palinurus.

**Fig. 124. A transverse section through a retinula in its middle region. The
lines of the retinular cells cannot be distinguished; the positio
each cell is marked by an irregular light mass in its centre.**

**" 125. A transverse section through a retinula in the plane of its ei
nucleus. Depigmented.**

Cancer.

(Figs. 126–131.)

**Fig. 126. A corneal facet viewed from its distal surface. The cuticula from w
this facet was drawn was cleaned by being boiled in a strong aqu
solution of potassic hydrate. It was examined in water.**

" 127. A transverse section of the distal end of a cone.

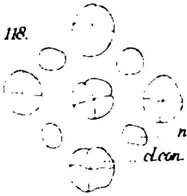
**" 128. A transverse section through three ommatidia at the level of the d
retinular nuclei. The pigment granules have been indicated in
the lower circle of cells.**

**" 129. A transverse section through the distal region of four retinulæ. In
two on the right, the pigment granules have not been drawn**

" 130. A transverse section through a retinula near the base of the retina.

**" 131. A slightly oblique section through the basement membrane. The u
part of the figure represents the retinulæ as seen in transverse
tion distal to the basement membrane; the part marked *mb*
represents the region in which the membrane itself appears in sec
and the lower half of the figure shows the cut fibres of the
nerve. The pigment granules are omitted from the right side o
figure. The transition from the retinular cells to the nerve f
is evident in passing over the section from top to bottom.**

118.



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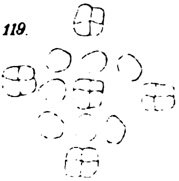

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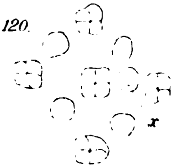

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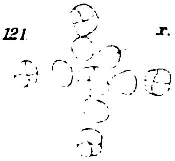

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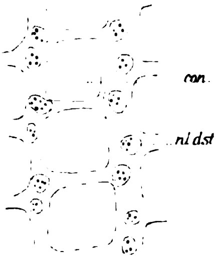

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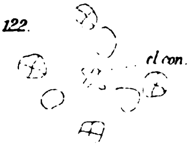

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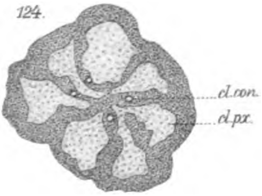

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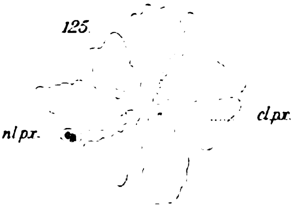

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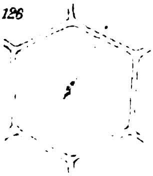

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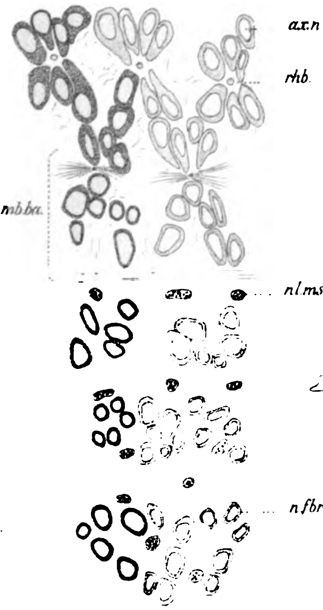

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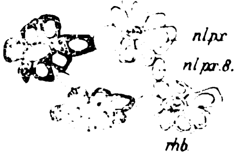

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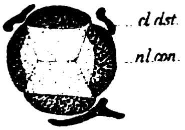

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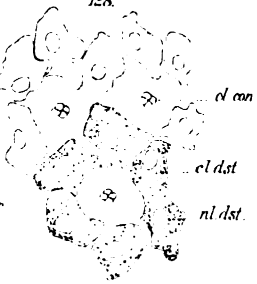

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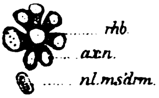

E. Meisel lith. Boston

DECAPODA.

Bulletin of the Museum of Comparative Zoölogy,
AT HARVARD COLLEGE.
VOL. XXI. No. 3.

26

ON SOME POINTS IN THE ANATOMY AND HISTOLOGY OF SIPUNCULUS NUDUS, L.

BY HENRY B. WARD.

WITH THREE PLATES.

7 CAMBRIDGE, U.S.A.:
PRINTED FOR THE MUSEUM.
MAY, 1891.

No. 3. — *On some Points in the Anatomy and Histology of Sipunculus nudus,* L. By Henry B. Ward.[1]

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Museum of Comparative Zoölogy, Cambridge, Mass.

With the compliments of

ALEXANDER AGASSIZ.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVI.

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I. Introduction.

Some two years ago, while working on Sipunculus nudus in the zoölogical laboratory at Göttingen under Prof. E. Ehlers, my attention was attracted by a peculiar organ in the region of the dorsal ganglion; and although it was a prominent feature of all transverse sections, no mention of its presence was found in the literature on Sipunculus. The observations made at that time interested me so much that the opportunity afforded by a short stay at the Naples Zoölogical Station last spring, for which I am indebted to the great kindness of Prof. A. Weismann and the Cultusministerium of Baden, was embraced to procure new, carefully preserved material. A study of the literature on Sipunculus revealed such lack of agreement between authors that a more general study of the form seemed likely to yield results, and, on the advice of Prof.

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E. L. Mark, a more particular consideration of some moot anatomica and histological points was undertaken. This was unfortunately limite by the material on hand, which consisted merely of the anterior portio of the body, corresponding in general to the introvert of recent writers As this contains, however, nearly all of the important organs of th nervous system to which especial attention has been paid in this paper and as its separation from the rest of the body at the time of killin insured good preservation, it is hoped that the conclusions reached ma not be without value, in spite of their incompleteness. The histologica structure of the body wall and of the nervous system has been treate in detail, and from the results an attempt has been made to throw som new light on the systematic position of the Sipunculids.

METHODS.

The material used in these investigations was preserved with especia care, and every effort was made to procure a method of killing whic should afford a clear idea of anatomical and histological relations unde normal conditions, since many of the contradictory statements of various writers have been undoubtedly the result of studying specimen in a distorted state, due to muscular contraction, or have followe the examination of tissues poorly preserved. The thick impermeabl cuticula, and the wealth of muscular tissue in the body wall, render it difficult matter to avoid at the same time both evils. The metho finally adopted as yielding the best results is as follows.

After remaining some time in clean sea-water to clear tentacles, bod wall, and œsophagus of adhering sand, the animals were brought int a shallow dish of sea-water, and 5% alcohol was allowed to flow gentl over the surface, forming thus a thin film, which disseminated itse gradually, and produced in the animals a complete relaxation of th body muscles. It did not seem to answer equally well when the alcoh and water were mixed at the start, as has been recommended for som animals. The length of time necessary for the attainment of complete narcosis cannot be exactly given. It varies greatly with differen individuals; but if, after lying some four to eight hours, the animals mak no contractions on being gently probed with a dull instrument, they ma be regarded as sufficiently stupefied, and transferred to 50% alcoho After a short stay in this, the introvert was cut off, and this alone subjected to treatment with higher grades of alcohol, which insured the penetration and consequent good preservation of the tissues. The only poin in the process which requires especial care, and which often produce a disappointing failure, is the transfer from the salt water and its added alcohol to 50% alcohol. If the animal is but partially narcotized, the muscular contraction induced by the transfer will spoil the specimen. If, on the other hand, it be left too long, the weaker parts of the body wall, especially the upper smooth zone of the introvert, swell out quite rapidly (through osmosis?), and not only the external form but the histological elements as well are badly distorted. The golden mean between these two extremes yields specimens as excellent for histological work as for the study of external relations. Material preserved in this way may be well stained by all methods. Where any stain has been of especial value in the study of particular organs or tissues, it will be noted under the topic in question. In this place I wish to express my thanks to Prof. E. Ehlers of Göttingen and to Prof. A. Dohrn of Naples for past favors, and to Mr. A. Agassiz, Prof. E. L. Mark, and Prof. E. B. Wilson for more recent kindnesses in supplying me with material for this study.

II. External Anatomy.

Selenka ('83, p. 92) has given a full description of the external characters of *Sipunculus nudus*. There are however numerous points of interest which first appear in a well expanded specimen, and which deserve especial attention. The body consists of a large posterior region covered by the quadratic integumentary areas (Hautfelder) and of a portion anterior to these, which is called the introvert.

1. INTROVERT.

This includes on the average one sixth of the entire length of the animal, and has in general the shape of a truncated cone (Fig. 1), the anterior base of which, only a little less in diameter than the posterior, is surmounted by a wreath of tentacles which nearly encircle the mouth. This region is ordinarily found entirely, or for at least two thirds of its length, invaginated into the following portion of the body, and is only rarely seen extended. In the latter condition it measures from three to four centimeters in length. The circular muscle bands, which are separate in the posterior part of the body, are here fused into an unbroken sheet of muscular tissue. The fusion takes place abruptly, and causes the immediate cessation of the integumentary areas (Hautfelder) due to the banded musculature, thus fixing a definite posterior boundary to the introvert. On the latter one can distinguish (Fig. 1) four regions:

(1) a posterior papillate zone [1] (*z. pap. p.*), (2) a smooth zone (*z. l*
(3) an anterior papillate zone (*z. pap. a.*), and (4) the tentac
crown (*pli. ta.*).

The posterior papillate zone occupies the posterior half of the in
vert, and shows a posterior portion, which is thickly studded with papi
and is dark brown in alcoholic specimens, and an anterior part m
lighter in color, where the papillæ are somewhat scattered. The ligh
almost translucent appearance of the anterior portion of this zone, wh
permits the central mass of the œsophagus and retractors to sh
through as a dark band, is due to the great diminution in thicknes
the muscular layers. The line of demarcation between the lighter
darker portions of this zone is somewhat definite, and is marked in
nally by the fusion of the longitudinal muscles into a continuous sh
and by the entrance into the body wall of the first large composite ne
given off from the ventral nerve cord (*cf. infra*).

The papillæ of this region are all shaped like the bowl of a spoon w
the concavity directed toward the body and the tip posteriad. Adjac
to the integumentary areas they are closely crowded, and overlap
the shingles of a roof, so as to hide the skin completely. They var
size and shape, but are in general broadly pointed, measuring on
average .25 mm. in length, and .65 mm. in breadth.[1] Passing forw
this general form is preserved until the point of transition from the d
to the light portion of this posterior papillate zone is reached. Here
papillæ grow abruptly smaller in absolute size, though relatively lon
and narrower, until the characteristic mammiform papilla of the li
region is reached. These only are represented in Figure 1. They
much lighter in color, and much less crowded, than the posterior papi
and leave irregular patches of skin entirely free. In breadth suc
papilla measures .25 mm.; in length, .37 mm. I am unable to conf
the statement of Andreae ('81, p. 205), that they are arranged
gleichen Abständen"; for the relative distances are extremely varia
being from 70 to 300 μ in the anterior portion of this zone. I was
unable to find the arrangement in a double spiral reported by Vogt
Yung ('88, p. 381). There seemed to be in fact no regular arrangem
common even to a majority of the specimens examined.

Passing forward, the papillæ grow ever sparser, and finally termin
along a well defined line, which marks the beginning of a smooth z
(*z. lev.*, Fig. 1) entirely free from papillæ. It measured 7 mm. in brea
in a specimen which had an introvert of 4 cm. total length. Anterio

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[1] The posterior half of the posterior papillate zone is not shown in Figure 1

this is a zone (*z. pap. a.*) with small papillæ; this measured 3 mm. in breadth in the same specimen. The papillæ of this zone appear superficially as minute discoidal elevations of the skin. In well expanded specimens, the tentacles droop over and nearly cover this zone, which is not separated from their base by any definite line, since the papillæ extend forward a short distance over the aboral surface of the tentacles, becoming gradually less frequent. They are indeed met with occasionally on the whole of this surface, but are entirely wanting on the oral aspect of the tentacles. In all well expanded specimens these regions are as well defined as in the one which has served as the basis for this description, and the zones have the same relative size as in the measurements given.

2. TENTACULAR FOLD.

The tentacles (Tentakelmembran) originate in the larva as two folds of the oral margin, — "lippenartige Falten," Hatschek ('83, p. 115), — separated dorsally but continuous ventrally, and lying right and left of the median line. Starting, then, from this primitive condition, the form found in the adult would be reached, if it be supposed that these flaps of skin are plaited radially to the oral centre, and that the growth is more rapid on the oral surface as well as toward the margin, thus necessitating a reflection of the flaps back upon the aboral surface. For a careful examination shows that in well expanded specimens the so-called tentacles consist of a thick fold of skin surrounding the terminal oral orifice with numerous plaits and folds arranged radially. This continuous flap may be called the tentacular fold, in preference to membrane, since the latter suggests a false idea of its nature, and its subdivisions may conveniently be termed the radial plaits.

The general form of the tentacular fold, as viewed from above (Fig. 2), may be said to be that of a horseshoe with the smaller dorsal curvature interrupted on the middle line. The external or ventral semi-circumference is reflected over the superior portion of the introvert, whereas the internal or dorsal portion makes a ventral flexion over the mouth, and lies higher than the other half of the tentacular fold. The superior height of the dorsal portion of the flaps in the larva caused Hatschek ('83, p. 115) to regard this as the "Anlage" of the first pair of tentacles. He knew nothing, however, of the further development of this portion, which probably represents the origin of the dorsal horns, since separate tentacles do not exist. In the adult, at any rate, this region shows two horns (Figs. 1 and 2, *crnu. d.*) projecting ventrad over the oral aperture, and forming together the dorsal curve of the horseshoe. Brandt ('70, p. 22 assigned a horseshoe shape to the crown of tentacles, but this has bee declared false by later investigators.

This normal hippocrepian form is often distorted when the introve is only partially extruded, or when there is undue muscular contractio within the soft mass of the fold itself, and it is always more or le disguised by the secondary radial plaits into which the fold is throw The relation of these parts will be easily understood by comparin Figures 1, 2, and 3. It will thus be seen that the reflection of the te tacular fold, with its deep radial plaits, brings into prominence regio — the "triangular tentacles" of some writers — which alternate wit retreating portions, so as to impart to the margin the appearance being cut or toothed, especially if the contraction of the muscular el ments in this soft fold has drawn it somewhat out of shape. In fac the description uniformly given by systematic writers has represente the tentacles as a membrane with numerous marginal incisions. Th error is due in part to distorted specimens; the true form may be sai to be crenate.

Therefore one can speak of the formation of tentacles only in a ge eral sense. But the fold may be regarded perhaps as the simpler for from which, by the development of certain areas alternating with regio of reduction, the more highly specialized digitate tentacles might be d veloped. Only the main folds are represented in Figure 2. These ma be much complicated by the appearance of subordinate plaits, until th general plan is confused by a mass of detail. The more simple form proved, on microscopic examination, to have been the most successfull killed, in that the muscular elements were in a more perfectly relaxe condition. The aboral surface of the tentacular fold is concave, exce in the dorsal horns, where it is convex; it has the same radial folds the oral surface with which it is approximately parallel. Numerous lo circular ridges traverse the aboral surface, and bear in varying numb the small papillæ already mentioned. These ridges are not regular course or size, and evidently vary with the convexity of the tentacul fold. In the midst of these, on the dorsal median line, can be found o careful examination a small oval opening (Figs. 2, 3, *can. o. ceb.*). It often so hidden in the ridges of the aboral surface as to make its di covery a matter of some difficulty. The opening measures about 1 b 0.5 mm., with its long axis transverse, and is surrounded by an evide marginal ridge. This is the opening of the canal of the cerebral orga to be described later.

III. Histology.

1. Body Wall.

In the body wall may be found the following layers, beginning with the surface: (1) a cuticula, (2) a hypodermis, (3) a cutis, (4) the muscular system, covered internally by (5) a delicate peritoneal membrane.

a. Cuticula and Hypodermis.

The cuticula consists of a substance optically like chitin, but differing from this, as has often been pointed out, in being soluble in boiling KOH. It is further aberrant in the absence of cellulose, which has been shown by Ambronn ('90) to be characteristic of true chitin. Tests with chloriodide of zinc showed neither any trace of blue nor the subsequent pleochroismus described by that author for true chitin. This layer is undoubtedly the product of the underlying hypodermal cells, which are everywhere found in a single layer, and normally display a sac-like form, although, as mentioned by Vogt und Yung ('88, p. 383), they may by contraction or compression of the body wall be drawn out into the form of spindles. This has given rise, as they mention, to the erroneous interpretation of such groups of elongated cells as being sensory organs. In contradistinction to these authors, I do not find the proximal ends of these cells ordinarily continuous with fibres which extend to the muscular layer, and cannot agree with them in regarding the entire mass external to the muscles as one layer. For if one examines a transverse section of the body wall as seen in Figure 5, the majority of the hypodermal cells are seen to be clearly marked off from the underlying tissue by the cell wall. The fibres of this subjacent tissue, to be described later, often extend up to the bases of the hypodermal cells; but close examination in favorable regions shows the connection to be merely apparent. Often when these cells are crowded and distorted by near-lying glands, one is inclined to believe in an actual continuity of cell and fibre which cannot be demonstrated, and which, so far as I could find, is not present in less confused regions.

Lying partly in the hypoderm, but mostly below it, are the dermal bodies (Hautkörper), which are of three sorts. A description of these will be given in the account of the cutis, with which they are most closely associated. No further specialized cells of any kind were found, neither sensory cells nor peculiar nerve endings of any sort, and I am inclined to regard the claims of their presence as founded upon the examination of poorly preserved material. Several times it was observed that delicate filaments, branching from some nerve fibre of the skin, proceeded to the hypodermis and penetrated apparently undifferentiated cells; certainly the distal surface of these cells bore no sensory hair or bristle. But the exact manner of termination of the nerve filament remained in doubt.

b. Cutis.

In placing a cutis in the list of the layers of the body wall, I am not unaware that the two most recent publications on Sipunculus deny its presence. As already mentioned, Vogt und Yung ('88) regard the entire extra-muscular layer as hypodermal, while Andrews ('90) evidently discredits the existence of a cutis by omitting the name altogether. What, then, is the actual condition of affairs? In sections one finds (Figs. 4, 5) between the hypodermis and the muscular layers a mass of gelatinous tissue, traversed in all directions by fibres, and containing not only glands of various sorts, but nerve fibres and pigment cells as well. Thus, though varying greatly in thickness in different regions of the body, it may properly be regarded, in the light of the characters mentioned, as a true cutis. The principal part of this layer is the connective-tissue jelly, homogeneous in its consistency and forming the matrix in which the nerves and dermal bodies lie. It is traversed in all directions by a multitude of the finest connective-tissue fibrils, which anastomose but rarely. Occasionally a minute nucleus can be observed in the course of a fibre. Scattered nuclei of a larger size, connected with nerve fibres or amœboid cells, are not infrequent in this mass, and have been erroneously regarded as belonging to the connective tissue. Irregular amœboid cells with but one nucleus and of a different refractive index from the general mass are found, sometimes in considerable numbers, and are perhaps similar in nature to the leucocytes of the tentacles, to be described later.

c. Pigment Cells.

Besides these elements one finds multinuclear cells of irregular outline more or less filled with granules of a highly refractive character. These are the pigment cells, so characteristic of this group that they deserve special consideration. Andreae ('81, p. 209) has given almost the only description of these peculiar structures. He represents the pigment granules as closely packed in meshes of connective tissue on which nuclei may be observed. This appearance is no doubt due to poorly preserved material; the true nature of the cells, as well as the process of deposition of the pigment, can clearly be understood from a section such as is shown in Figure 5. The cutis contains here a group of irregular amœboid (?) cells, distinguishable from the surrounding mass by their refractive power, and containing from five to many deeply stained nuclei 3 μ in diameter. The cells are all without any proper membrane, though often surrounded by an envelope of connective fibres, and enclose a varying number of highly refractive granules distinguished by indifference to any coloring matter but picric acid, which they take up with great avidity. Their natural color by transmitted light is a greenish yellow; by reflected, however, a dull brown or yellow. That the process of formation is gradual becomes evident on the examination of a section like Figure 5. In some cells are seen only a few such granules, or they are confined to one part of the cell; and all stages are present from this up to a mass of closely packed granules in which neither cell plasma nor nuclei are visible. Even in such cells the nuclei could be demonstrated by prolonged staining and thin sectioning. The plasma of these cells shows at first some slight affinity for hæmatoxylin, which disappears as the granules become more crowded. In the first stages of deposition the granules are mere bright dots too small to be measured; in the more thickly crowded cells they have reached often twice or thrice the size of a nucleus, and alongside of these are also granules as minute as those of the earlier stage. Such cells are present not only in the cutis, but also in all other organs of the body. They are not always as numerous as shown in Figure 5; in the tentacles they are quite rare, whereas the nervous system contains especially large numbers in all its parts. Somewhat similar cells were found by Bürger ('90) in the nervous system of Nemertines. Wherever these cells are found in Sipunculus they display the same structure, except that elsewhere than in the cutis they are only found well filled with granules. Whether a migration actually takes place, as is suggested by their evidently amœboid character, I was unable to determine. It is to the presence of large numbers of these cells that the papillæ of the posterior zone and the walls of the cerebral canal owe their dark color. The pigment cells are present in much greater numbers in large than in small specimens, i. e. in older than in less mature ones. I can confirm the statement of Vogt und Yung ('88, p. 386) that fasting rapidly decreases their number. It is not a necessary conclusion that this is to be regarded as reserve material. For even waste may, under the pressure of failure in the food supply, be drawn into the system and worked over again.

d. Dermal Bodies.

Various opinions have been held by different authors as to the morphological value of the dermal bodies. Keferstein und Ehlers ('61) described them as glands, Leydig ('61) regarded them as sensory organs; but later writers have inclined to the former view. Andreae ('81) described three varieties of these organs, whereas Vogt und Yung ('88) made the claim that the sensory organs, Andreae's third variety, do not exist, and that all of the glands are merely modifications of one sort. As to the first statement, they are undoubtedly correct; but to the latter view I am unable to assent. The transition from one sort of gland to the other, though plausible from surface views such as given by those authors, is only apparent. For if one examines carefully prepared sections, the seeming similarity gives way to a well marked difference. Not one of the glands is actually unicellular, as claimed by Vogt und Yung, and the multicellular contain never less than five cells, which serves to separate them clearly from the other kind, which is always bicellular. Moreover, their behavior toward staining fluids is very different. For while the bicellular glands take up hæmatoxylin with such rapidity as to become almost black in a few seconds, the multicellular are but little affected by this reagent. Carmine solutions stain the two about equally, but bring out the nuclei, which are invisible in a hæmatoxylin stain. And, finally, the morphological elements of the two sorts are essentially different, as will be shown. The old classification of bicellular and multicellular glands will therefore be retained, and the structure of each will be examined more in detail.

The *bicellular glands*, when viewed, even in the living animal, directly from above, display a clear zone along the line of the partition wall between the cells. This is invisible if the gland be viewed from the side, or at a considerable angle, and gives rise to various images if the line of sight be more or less nearly perpendicular to the surface. As the papillæ which contain the glands have sloping sides, never exactly alike, it is easy to understand how views of the glands from many different directions may be had from a surface inspection, and how the various images may give the appearance of a series from the bicellular to the multicellular gland. If one examines, however, sections of the skin perpendicular to the surface (Figs. 4, 5), the bicellular glands appear at once as a distinct type. Ordinarily spherical, they may often be found mutually flattened where several lie closely pressed together. They vary in diameter from 40 to 50 μ, and present very different appearances according to the stain employed. The greatest number of structural details are obtained from those lightly stained with hæmatoxylin. Sections thus stained are represented in Figures 6, 7, and 8. Though evidently differentiated hypodermal cells, they lie almost entirely in the cutis, enveloped by a delicate coat of connective tissue, in which can be found occasional flattened nuclei. The distal half of each cell is occupied in great part by a large vacuole, directly continuous with that of the adjoining cell. The space thus formed measures $12 \times 15 \times 25\,\mu$, and communicates with the exterior by means of a narrow canal opening simply on the surface of the cuticula. The duct measures 6–8 μ in diameter, and at the distal end of the cell does not lie in the centre of the neck (Fig. 9). The connective-tissue envelope does not penetrate between the cells, which in consequence are separated *only* by their own membranes (Fig. 6 or 11,*), and these, continued over or under the distal vacuole, appear, if the cell be viewed along the plane of the partition, to bisect the vacuole (Figs. 6, 10); the latter suffers, however, a slight constriction along this line, so as to impart to it in transverse section a biscuit-shaped appearance (Fig. 7). Its longitudinal section is cordiform, as shown in Figure 6. The two large clear spherical nuclei, 9 μ in diameter (Figs. 10, 11), may be differentiated with carmine or saffranin, and then appear in the lower half of the cell, usually nearly symmetrical to the dividing membrane. Each displays a single central deeply stained nucleolus, and many minute chromatine granules. If the plane of the section pass transversely *below* the vacuole (Fig. 11), the cells are seen to possess a hemispherical form, and the dividing membrane to make an S-shaped curve.

Whether active or resting, a clear zone of plasma forms the periphery of the cell on all sides, and is therefore adjacent to the vacuole, as well as to the external surface of the cell. This zone is traversed radially by delicate fibrils, the beginnings of the plasma reticulum which fills the cell, but which ordinarily is easily seen only in this clear zone. In every section one finds a few cells of this sort, which, besides an empty vacuole, exhibit this reticulum very plainly throughout the entire faintly tinted cell body (Fig. 8).[1] They are evidently the functionally inactive or resting cells. The first stage in secretion is seen in the accumulation of numerous granules in the basal portion of the cell (Fig. 6), which are stained deeply with hæmatoxylin, and by continual aggregation finally obscure the reticulum, and impart to the entire cell, save its marginal zone, an appearance almost opaque (Fig. 7). The secretion first appears in the vacuole in the form of minute beads at the peripheral ends of the reticular fibrils which traverse the clear zone and terminate at the edge of the vacuole each in a single bead (Fig. 7). During the formation of the secretion in the vacuole, the mass of opaque granules moves toward this space; and the close of the process is represented in Figure 8, where the vacuole is filled with a homogeneous mass, displaying in a somewhat lesser degree the affinity for hæmatoxylin stains which characterized the granules while contained in the cell substance itself. At the same time, these granules have disappeared, except a few which are grouped in a zone about the vacuole; and the cell has become thereby so much lighter as to show the reticulum at its proximal end.

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[1] Strictly speaking, Figure 8 represents the *last* phase in secretion. The first differs only in the absence of matter in the vacuole, and of the few granules just below it.

This description of the activity of these organs would seem to place their glandular nature beyond question. In comparing the two sorts of glands, it is of great importance to note that the cells do not show in this case any connection with nerves, whereby they are sharply distinguished from the multicellular glands. The space (Spalt) which Andreae ('81, p. 215) describes as existing between the cells of these glands was found not infrequently in some preparations, but it is evidently due to shrinkage. The double membrane separating the cells, described by the same author, was probably produced in the same way.

The distribution of these glands is peculiar. Over the general surface of the body they are found only rarely, and on the introvert they are present only *in the papillæ*, the interspaces being entirely free from them. Each papilla of the posterior zone of the introvert shows in surface views an irregular double or triple row crossing the convex outer surface near the base, and occupying one half to one third of its entire breadth. Rarely isolated bicellular glands are found near the tip. This regular limited distribution allows perhaps a conjecture as to their possible function. Inasmuch as the behavior of the secretion toward coloring reagents would seem to mark it as mucine (cf. Hoyer, '90), may it not be that these glands furnish the lubricant demanded by the constant movements of the two walls of the introvert? The papillæ are especially affected, of course, rubbing against each other in the constant inversion and eversion. They receive, furthermore, the greater part of the pressure as the animal forces its way through the sand, in the method described by Andrews ('90, p. 391). The animal does not advance backward with the "Eichel voran," as maintained by Andreae ('81, p. 220)! The secretion may also be of use in cementing the sand grains into a sort of tube noticeable when the animals are dug out of the sand.[1]

The *multicellular glands* present a type easily distinguishable from that just described. They are to be met with everywhere, not only in the papillæ, but lying in the interspaces as well, and extending up into the clear zone of the introvert, where they are the only differentiated hypodermal cells. Never much crowded, they become here sparser, until they completely disappear at the level of the upper papillate zone; nor are they to be found in or above this zone, nor at any point on either surface of the tentacular fold. The multicellular glands may be identified on surface preparations, but an insight into the histological relations is first afforded by sections. With hæmatoxylin the cell body stains lightly but uniformly, the mass at the distal end more deeply (Fig. 12), but with this stain no nuclei can be found either in the cells or in the connective-tissue investment of the gland. Each gland is seen to be made up of a number of flask-shaped cells, which are separated by thin partitions and which unite at their distal ends into a duct piercing the cuticula and opening upon its surface to the exterior. Andreae ('81, p. 216) was unable to find any nuclei in these cells. The application of a carmine stain, however, shows their presence near the proximal ends of the cells (Fig. 14), where they often lie flattened against the cell membrane by the crowding of the granules accumulated in the cell plasma. The same stain demonstrates also (Fig. 13) smaller nuclei at various points in the connective-tissue investment. There is likewise seen to be a difference in the cells of any one gland which indicates alternation in secretive activity. Thus the plasma of some cells is thickly crowded with large granules, which are entirely wanting in other cells. This is most clearly demonstrated in a transverse section of the gland, as shown in Figure 13. The cells differ in intensity of color to correspond with the number of granules present, and large distended cells are found near those which are evidently thinner and poorer. The product of these glands is a substance more waxy than fluid, to judge from its manner of caking in the duct, and breaking up into small fragments, like sebaceous material. Its discharge is evidently gradual like its production; for I have never found a gland empty, nor does the total amount of secretion present vary greatly. This alternation in functional activity between the various cells of one gland and the constancy of secretion from the gland as a whole stand in strong contrast with the resting and active stages in secretion as found in the bicellular glands. The function of the secretion from the multicellular glands is probably more general, since the glands are so uniformly distributed over the surface of the body.[1]

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[1] For this suggestion, and the observation that such a tube exists, at least for S. Gouldii, I am indebted to my friend, Mr. C. B. Davenport.

One of the most peculiar points in connection with these glands is their relation to the nervous system. In almost every instance, a nerve fibre can be clearly traced from the subdermal plexus to the proximal end of the gland, and on fortunate sections (*gl.'''* *n. fbr.*, Fig. 14) it was possible in a number of cases to demonstrate an actual connection between gland cell and fibre, in that the former was prolonged into a delicate fibril, which, passing out from the glandular cavity in company with similar fibrils from the adjacent gland cells, entered within the neuroglia into the substance of the nerve and appeared to make up its fibrillar structure. This connection of gland cell with nerve fibre is found in all regions of the body, and is not confined, as Andreae maintained, to the posterior tip (Eichel) of the animal. In spite of this direct nervous connection, there seems to be little ground for regarding these structures as sensory organs, the interpretation put upon them by Leydig ('61) and others after him. A careful examination brought to light only the single kind of cells, which are in no way comparable with sensory cells. On the other hand, it may be said that a rich nervous supply is not without parallel for glandular structures.

The capsules of these glands are very thick, and nuclei are found on the partitions between the cells, showing that each cell is enclosed in a separate investment. But the partitions are never as strong as the general sheath of the entire gland, which possesses nearly the optical appearance of muscular elements. The variations in size are so great, being from 40 × 50 μ to 90 × 150 μ in the same region of the body, that the probability of a muscular capsule suggests itself strongly.

Allusion has already been made to the relation of the glands to the papillæ. In each papilla of the posterior zone, one finds at its tip an indefinite crowded mass of multicellular glands, and in an irregular double or triple row across the basal half, the bicellular variety. All of these open upon the external convex surface of the papilla. That the relation of glands to papilla is an intimate one, first appears clearly from the formation of the latter. As it is evident that new papillæ must be added with the growth of the animal, it is of interest to note the steps in the formation of these structures. The first indication is an evident crowding of the otherwise scattered multicellular glands in the centre of some interspace of more than average size. Then the bicellular glands make their appearance as a loose double row, and so quickly that no intermediate stage could be found. They grow more crowded, and soon after their appearance a shallow furrow may be seen to enclose the mammiform area which they occupy. The skin seems to be tucked in on the three sides at once, and as the furrow grows deeper the papilla becomes more and more prominent. The growth in any papilla is increase in breadth rather than in length, so that the relative dimensions gradually change, and the older papillæ in any region are markedly wider than those more recently formed, while the length remains nearly constant throughout the entire zone.

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[1] See Addendum.

Sense Papillæ. — The papillæ of the anterior zone are thickenings or modifications of the hypodermis, rather than typical papillæ like the posterior ones; they correspond probably to the "Wimperdrüsen" of Vogt und Yung ('88, p. 406). They are externally marked as small rounded prominences of the skin, varying in diameter from .15 to .40 mm., and often exhibit an oval or dumbbell-shaped opening in the centre of the prominence. Viewed in cross section (Plate II. Fig. 18) they display an evenly rounded contour, which is surmounted by cilia. These are short on the lateral margins of the area, but increase in length as they approach the apex, where they are longest. If one notices the basement membrane, here for the first time well developed, it will be seen that the prominence is almost entirely due to the increased height of the hypodermal cells, which have changed their form from that of the usual hypodermal elements so as to assume the character of filamentous cells, such as compose the hypoderm of the tentacles, with which they are identical. The isolated elements of the latter (Plate II. Fig. 21) might, indeed, answer equally well as types of these cells. In addition to the elongated nuclei of these cells, some few rounded ones are seen scattered between the filamentous cells, more usually near the basement membrane. Perhaps more common than the normal expanded form of the papillæ, just described, is the retracted condition shown in Figure 17. Such are found in all degrees of contraction, alternating irregularly with the normal form. The papilla figured is perhaps fully retracted, and one notes that the apical area lies sunk in the structure, so as to give the effect of a cavity and a duct. That this is due in part to the contraction of the cells themselves, and in part to the retraction of the central portion of the papilla, is clear from a comparison of Figures 17 and 18. In spite of this, I was unable to identify any muscular elements connected with the organ, the many fibres which are attached to the proximal side of the basement membrane being, in refractive power and other optical properties, and in the character of their nuclei, indistinguishable from the other cutis fibres. One often finds such an appearance as is given in Figure 16. This is evidently a tangential section of a similar organ; the central clear space represents the hollow produced by the retracted apical area, and the apparently round nuclei are merely the elongated forms transsected. The appearance of the cells suggests no glandular nature, and nothing could be found resembling a secretion. For this reason I am inclined to question the propriety of the name "Wimperdrüsen" (Vogt und Yung, '88, p. 406), and to regard them as simple sensory organs. The retraction of the apical area would then be a simple method for protecting the long and delicate cilia during the advance of the animal through sand, similar to that reported by other observers for such organs in various groups. I was unable to discover any nerves connected with these organs, so that their sensory nature remains unproved, although none the less probable (Eisig, '87, p. 548). The structures just described are distributed over the aboral surface of the tentacles in somewhat irregular lines, becoming less frequent toward the margin of the fold, but are not present on its oral aspect. They suggest strongly the diffuse sensory organs (Becherorgane) of Capitellidæ, described by Eisig ('87, p. 547), but they are certainly less highly differentiated in the following respects: — 1. The cilia are not confined to the apical area (Polfeld), but are more or less diffused over the entire prominence. 2. There are only a few of the nervous nuclei (Körner) present in the basal portion. These structures recall the cup-shaped organs of Capitellidæ most strongly in the character of their elements, the filamentous cells, in their relation to the general hypodermis, and in the thin cuticula which covers them. In both cases, connection with nervous elements remains a matter of conjecture.

Very similar organs have been described by Spengel ('80, p. 465) for Echiurus, as appears at once from a comparison of the figures given by that author (Taf. XXIV. Figs. 21, 22). These, however, differ materially from those in Sipunculus in two respects: first, no cilia were present (Spengel believes them to have been lost through poor preservation); secondly, a fact of more importance, a large number of unicellular glands are found immediately below and in connection with these organs in Echiurus. The latter are certainly not present in Sipunculus. The distribution of these organs is quite different in the two forms, since there occur from one to seven on each of the papillæ of Echiurus, whereas in Sipunculus they are confined to the small anterior zone of the introvert.

e. Muscular Layers.

Of the muscular layers the diagonal is not present in the introvert. The circular layer, which is banded throughout the rest of the body, fuses at the end of the integumentary areas into one continuous sheet, and grows gradually less important anteriad, being almost entirely wanting in the anterior zones. The longitudinal muscular bands do not fuse until the middle of the posterior papillate zone is reached. From this point anteriad they also become reduced so that in the smooth zone the entire muscular layer measures but 70 to 90 μ in thickness. This remnant passes over into the retractors in a manner to be described in treating of the tentacular musculature.

2. TENTACULAR FOLD.

A cross section of the tentacular fold shows that it consists of two layers of skin, which form the oral and aboral walls of an irregular cavity, traversed perpendicularly by numerous trabeculæ binding the two sides together (Fig. 3). This cavity is the extension of the so-called blood system, and is often found more or less filled with a coagulum. The character of the oral and aboral walls of this cavity differs: the structure of the oral portion will be considered first.

a. Oral Wall.

The cuticula (Plate III. Fig. 23) is extremely thin, never exceeding 2 μ, and usually appearing as a fine double contour. It is pierced by many pores for the exit of the fine cilia, which cover this surface from the apex of the fold down into the mouth. Evidently the inversion of surfaces in the retracted condition of the introvert led Selenka ('83, p. xvii) and others to regard the oral surface of the tentacles as without cilia, and to maintain that the aboral surface was ciliated, exactly the reverse of which is true.

The hypodermis (Plate III. Fig. 23) is composed of very high cells, which are in contact merely by their distal ends. Proximally they are prolonged into delicate processes, by which they are attached to the basement membrane. These cells are of the type of filamentous cells (Hautfadenzellen) described by Eisig ('87, p. 300). Lying nearly in the centre of the cell is the elliptical granular nucleus, which measures 11 by 4 μ. These cells are exactly similar to those contained in the sensory organs before described. Some such cells are seen in Figure 21, *d*, *f* (Plate II.). In addition to these there are occasional cells in the hypoderm, the nuclei of which are narrower and stain much deeper, which possess a denser, more highly refractive cell body. Figure 21, *a*, *c*, *e*, represents these cells, which are seen *in situ* at *cl. sns.*, Figure 23. These may be sensory cells; I was, however, unable to discover the sensory hairs described by Selenka ('83, p. xvii) as found on the external surface; these cells certainly possessed merely such cilia as those adjacent. At the level of the mouth there is a transition from these filamentous cells to the columnar cells of the intestinal tract. This serves to fix the level of the oral opening proper, which would otherwise be indefinite on account of the various degrees of expansion or contraction of the animal.

b. Migratory Corpuscles.

Between these filamentous cells are found at varying heights highly refractive spherical nuclei 4 μ in diameter. My attention was first called to them in a preparation stained by Hamann's carmine (Plate II. Fig. 15), where they become prominent by reason of their being stained deeper than the other nuclei. A more careful examination showed that they were not accidental, as at first surmised, but definite independent structures. Each is surrounded by an irregular clear zone varying in width from a mere line to one half the diameter of the nucleus. By means of these peculiarities, such cells were traced back through the cutis, where they were most abundant in the spaces just below the basement membrane, to the blood cavity, and were found to agree precisely in size and optical character with one kind of blood corpuscle found in the coagulum there. They may then be regarded as migratory corpuscles or leucocytes, analogous perhaps to those of vertebrates. Similar cells are often met with, though never in such numbers, throughout the body wall.

The thin basement membrane to which the processes of the filamentous cells are attached is not everywhere equally distinct. Owing to the contraction of the different areas, it may be thrown into extensive and complicated folds, which, combined with the basal processes of the filamentous cells, render its identification a matter of difficulty, but in suitable regions it may be identified beyond a doubt.

Beneath this membrane lies a cutis, very similar to that of the body wall. It differs chiefly in the scarcity of pigment cells and in the entire absence of glands. The "Wimperdrüsen" seen by Vogt und Yung ('88, p. 406) on the oral surface of the tentacles, are merely appearances due to unequal contraction of certain areas, which produces structures superficially similar to the sensory organs of the anterior papillate zone already described. The cutis is further peculiar in the possession of numerous muscular elements, which are primarily arranged about the blood cavity. The relation of these to the body musculature is of considerable interest.

c. *Musculature.*

If a transverse section be made in the plane of the annular mass of muscle surrounding the pharynx which is produced by the fusion of the four retractors, there appears only an indefinite mass of confused fibres. If, however, the section be cut in any longitudinal plane, it will be seen that the longitudinal fibres which compose this mass divide into two unequal parts, each of which draws its fibres from all parts of the original muscular mass. In such sections each of these portions appears like a band; the smaller curves over into the muscularis of the body wall of the introvert, or rather goes to form the longitudinal muscles of this, its fibres being directly continuous with those of the predominant longitudinal layer. The other and larger portion ascends into the tentacular fold; a few of its fibres follow the aboral surface of the blood cavity, but by far the greater number are continuous as an apparent muscular band along the oral side of the cavity immediately adjacent to the latter. At the base of the tentacular fold it is thickest, measuring half the thickness of the oral wall in which it lies; but as it advances distad through the tentacular fold, fibres are continually given off peripherally, so that they radiate toward the surface. These terminate in the vacuolated portion of the cutis in some manner not exactly determined. In this way the muscular band becomes looser and looser by the gradual loss of its elements, until at the tip of the tentacle only a few fibres remain, which attach themselves there. In cross sections the tentacular fold shows a few circular fibres, immediately adjacent to the blood cavity, which turn into the trabeculæ and cross into the corresponding layer of the opposite wall of the fold. In addition to these, the trabeculæ have other fibres which cut the muscular band at right angles, and run from one side of the tentacular fold to the other. At the outside of the muscular band there can be found usually a few circular fibres. If one considers that this muscular band, prominent in longitudinal sections through any plane, thus represents a muscular sheet extending throughout the whole tentacular fold, and that this lies in the cutis of the oral, or in an expanded condition *convex*, surface of the blood cavity, with its fibres radiating into every fold of the tentacles, — if one remembers, further, that it is at its base connected with the fused retractors, and is in fact merely an extension of them, — then its action in the inversion of the tentacles by drawing in and packing together the various folds and plaits becomes at once clear. Furthermore, th muscles concerned in emptying the blood cavity are primarily the powerful trabeculæ and the longitudinal muscles, whereas the circular muscles which are comparatively scanty, are only of secondary importance.

The cutis of the oral fold contains also numerous vacuoles in group near the basement membrane, and these may be seen in transverse sections filled with the migratory cells previously mentioned. In additio to these small leucocytes, occasional larger granular cells are found i the lacunæ. These correspond again to the granular corpuscles of th blood. They do not make their way into the hypodermis. A tissu which might be homologized with the supporting tissue of Phoronis doe not, according to my observations, exist in this form.[1]

Lastly, lining the blood cavity and covering the trabeculæ is an endothelium of very flat cells with proportionally large nuclei. This endothelial lining is continuous, and is adjacent to a mass of gelatinou connective tissue, which is without vacuoles, so that the blood corpuscle could reach the hypodermis only by a definite migration through th endothelium and the connective tissue. The cavity is often distende by a coagulum which contains corpuscles that, as various writers hav maintained, actually differ in size from those of the cœlomic fluid, s that a connection between the two cavities was regarded as improbable I can confirm the statement of previous writers that no such connectio exists. Yet as the corpuscles are in size between the extremes of thos in the cœlomic fluid, and not far from the average (*cf.* the exact measurements of Brandt, '70, p. 3), it is not improbable, in view of th migratory tendency of the corpuscles already described, that the cœlomi fluid receives its quantum from the blood system by the active emigration of the corpuscles which are formed in that system. This was conjectured by Brandt ('70, p. 24), who had found, however, no evidence o such a tendency on the part of the corpuscles. The detailed and carefu account of the vascular system given by him has been overlooked b many later investigators.

d. Vascular System.

In contradistinction to Sipunculus Gouldii and to Phascolosoma, th blood cavities of S. nudus are not in the form of regular vessels, bu are indefinite lacunar spaces, traversed by trabeculæ at irregular intervals and extending throughout the whole tentacular fold, everywher almost equally distant from the exterior.

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[1] See Addendum.

Numerous facts have been adduced by Andrews ('90, p. 419) to prove he branchial nature of the tentacles in S. Gouldii, chiefly the circulation nd the red coloring matter of the corpuscles. Certain structural and ther peculiarities compel me to deny the respiratory nature of this ystem in S. nudus. As was pointed out by Brandt ('70, p. 23), the xtreme thickness of the layer of connective tissue in the tentacles ould militate against the opinion that respiration takes place to any onsiderable extent in this part. Furthermore, although I have watched . nudus in aquaria for considerable periods of time, not only when they ere lying upon glass, but also when they were on the surface of the and, and in their burrows wherever these were adjacent to the glass so s to permit observation, I have seen the tentacles extruded but seldom, nd never for more than a second or two, until the water had become so mpure as to partially narcotize the animals. The respiratory value of he tentacles when retracted cannot be regarded as very important!

But the greatest objection to assigning a respiratory character to this ystem would seem to be the utter inadequacy of the internal mediation etween the vessels and the cœlomic fluid. The possible importance of his system in a respiratory direction must be seriously questioned when ne considers that the ring canal and the two blind sacs (in S. Gouldii ut one!) buried in the connective tissue of the œsophagus, which at est expose but one half their surface to the cœlomic liquid, are the nly means of transmitting oxygen from the so-called vascular system o the general body fluid. The observations of Keferstein ('62, p. 47) pon living animals — these were made on Phascolosoma elongatum of a ew millimeters in length and fully transparent — showed a constant movement of the fluid, but no passage of it from the vessels into the tentacles, r *vice versa,* except under considerable pressure or violent injuries.

The probable lack of respiratory function in the vascular system cannot be extended to all Sipunculids. In this connection it is of great nterest to notice that various species are provided (Selenka, '83, p. xix) ith several or many branched lateral appendages attached to the blind ac. Such organs are found in Phascolosoma Semperi, P. maniceps, hymosoma asser, Dendrostoma signifer, *et al.* All of these forms possess, according to the same author, long thin filamentous tentacles *cf.* his generic descriptions and figures). This peculiarity suggests at nce the probability of a respiratory nature for the tentacles; and its ccurrence in single species of various genera would indicate that it is a econdarily acquired function.[1]

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[1] See Addendum.

The numerous dermal canals close under the hypodermis of S. nud are unquestionably of great value in respiration, and the region of t introvert, which is distinguished by thin cuticular and muscular laye actually not so thick as the walls of the tentacular fold, presents a f greater surface for the transmission of oxygen directly to the cœlom fluid than the entire vascular system.

Primarily, then, this system is hydrostatic, and this is probably i chief function in S. nudus. The dorsal and ventral vessels are rese voirs into which the fluid is driven by the contraction of the tentacul fold. On the other hand, the muscular walls of these vessels serve force the fluid out into the lacunæ of the tentacular fold, and thus move and expand the latter. The varying contraction of these two se of muscular elements gives rise to the constantly changing form of t tentacles, as the fluid is driven to and fro. This movement might easi simulate, or even under certain conditions become, a circulation. Mor over, any method of killing which worked violent contraction would di tort the tentacular fold by driving the fluid into the extreme distal en of the lacunæ, or by drawing together the entire mass of the tentacul fold, and forcing the fluid back into the dorsal or ventral vessel. It probably in this way that the lobed or cut form was produced, whic has been given as the typical one in all generic descriptions hither published. It is worthy of notice that those animals which were kille with expanded tentacles showed the walls of both dorsal and ventr vessels almost in contact, whereas in those which had retracted the tentacles these vessels were so filled by masses of coagulum as to reac a considerable diameter. The probable function, then, of the dorsal an ventral vessels is to receive and hold the fluid forced out of the tent cles at the time of inversion of the introvert.

e. Aboral Wall.

The aboral wall of the tentacular fold differs from the oral chiefly i the undifferentiated condition of the hypoderm. The latter is here com posed of low non-ciliated cells, identical with the hypodermis of th general body wall, except where it is elevated into the papillæ or sensor organs already described. Sensory cells are wanting. The cutis of th aboral wall lacks the vacuoles which characterize that of the oral wal and there are only very few leucocytes to be found.

The thin cuticula, cilia, and sensory cells of the oral, as well as th general sense organs of the aboral, wall of the tentacular fold, show it t be a most important organ of touch. This view is strengthened by th large nervous supply it receives from the brain direct. The cilia undoubtedly aid in propulsion of food particles into the mouth.

3. Nervous System.

a. Brain.

The supracœsophageal ganglion (*gn. su'œ.*, Fig. 3) lies dorsal to the blood sinus, between the two dorsal retractors, and is enveloped by an investment of connective tissue. The posterior surface (Plate II. Fig. 22) is marked by a considerable incision in the median plane, and the anterior dorsal margin bears numerous digitate processes, which project into the cœlomic liquid. In sagittal sections the brain appears nearly flat on its ventral side, whereas the dorsal aspect is considerably curved. As seen from transverse sections, however, the dorsal surface is plane, while a deep median furrow (Plate III. Fig. 25) penetrates the ventral wall. Posteriorly (Fig. 25) this is continuous with a partition which divides the brain into two symmetrical lobes. Anteriorly (Fig. 24) the partition fails, and the division is only indicated by the furrow. On the antero-ventral surface is the termination of the cerebral canal (*cf. infra*).

The entire ganglion is covered by a capsule (Fig. 25, *cps. enc.*), the origin of which can only be determined by the consideration of a series of transverse sections. Following such a series from a short distance posterior to the brain, it will be seen that the septum joining the two dorsal retractors is here fused with the dorsal wall of the œsophagus, in which lies the dorsal vessel. As the posterior extremity of the brain is reached, this septum rises upon the brain, covering its dorsal aspect, and still showing laterally the connection with the dorsal retractors. Immediately inferior to the brain lies the dorsal vessel (Fig. 25, *va. sng. d.*), or, anterior to this, the blood sinus, which is separated from the brain only by its own wall, which thus forms the ventral covering of the brain. The dorsal and ventral layers of the capsule are continuous on those parts of the lateral aspect of the brain where there are no outgoing nerve stems; but when the latter exist, a neighboring portion of the brain capsule is reflected over them to form the neurilemma (Fig. 25, *con't. tis.*). This composite capsule is made up of a loosely woven mass of fibres which often show a plaited arrangement. The discoid nuclei measure 3.5 by 5 μ, and are deeply stained in all coloring fluids. Inferior to this basketwork of fibres are found occasional nuclei, which stain very faintly and possess each a few small nucleoli. These are surrounded by a small amount of a granular substance, and are very similar to nuclei found in the midst of the meshes of the brain itself. Passing inward from this external capsule and directly continuous with its elements, fibres penetrate the brain in every direction, either in definite strands, or in a delicate network surrounding the ganglionic cells (Fig. 25). The fibres which make up these meshes are finer than most of those composing the capsule itself, and recall strongly the finer elements of the cutis. With these they also agree in the possession of minute elongated nuclei, although the clear nuclei previously mentioned are by no means rare. These fibres surround each ganglionic cell with a definite covering (Plate III. Fig. 32) of interlacing elements from which others pass off tangentially to neighboring cells. (*Cf.* Rohde, '87, Taf. IV. Fig. 44–68.)

Ganglionic Cells. — None of the many previous writers on Sipunculus have considered the histological elements of the central nervous system more than cursorily, so that a more extended description of these may be of interest, especially for comparison with the recent exact determination of these elements in many other groups of worms. All the ganglionic cells which were so situated as to admit of a positive answer to the question of their polarity were unipolar, though by no means always unifilar. Such cells as were accurately determined were usually peripheral, since the mass of other fibres and the confusion of many cells make an accurate determination in the case of those cells which are located in the centre of the nervous mass often impossible. I am inclined to think that in the latter region there are multipolar cells, although the demonstration of these was not wholly satisfactory. The cells are uniformly without any proper cell membrane. Each lies enveloped in a covering of delicate connective-tissue fibres (Plate III. Fig. 32), which accompanies the fibrous processes in the form of a delicate sheath (neuroglia). These enveloping fibres are a part of the meshwork which has already been described as arising from its external capsule, and penetrating through the whole brain.

Of all the ganglionic cells, the smallest (Plate III. Figs. 24, 25, *cl. gn. I.*), which usually appear simply as nuclei measuring 6 by 4 μ (Fig. 30), are the most abundant. They are highly refractive, and show a great affinity for coloring matter. There is a nuclear membrane which is stained deeply, as are also the numerous (4 to 10) nucleoli; between the latter many minute chromatine granules are distinguishable with a high power. These nuclei seem somewhat irregular in shape, varying from circular to oval. This variation I regard as due to the direction of the plane of section, and consider the true form as oval. In most cases it is impossible to find even a trace of a cell body, and I was at first inclined to doubt the presence of any recognizable cell substance, and consequently to compare them with the "Nervenkerne" described by Rohde ('87, p. 30). But at length fortunate staining and thin sectioning showed unmistakably the presence, in many cases at least, of an extremely small cell body, such as is shown together with the nerve fibre in Figure 31. It will be noticed that the nucleus is oval in this case, and that the nerve fibre proceeds from one of the small ends of the oval. This fact, as well as the variation in form noticed by careful focusing on the nuclei, would seem to warrant the assumption that these nuclei are uniformly oval. From the diminutive size and transparency of the cell body in comparison with the highly refractive nucleus, it is at once evident that the former can be seen only under the most favorable circumstances. Since I was unable to find any difference in position, size, or optical qualities between these and the other nuclei of similar size and appearance, I feel justified in maintaining the existence of such a cell body for all nuclei of the class.

The second sort of ganglionic cell (*cl. gn. II.*) is distinguished by the presence of a much larger cell body (Plate III. Fig. 29). The nuclei correspond so exactly to those of the first class that they can hardly be distinguished from them. I was unable to see that they were either more or less deeply stained, or that they were, on the average, larger or smaller than nuclei of the first sort. The great difference is in the cell bodies, which in this case are several times larger than the nucleus, measuring 20 by 14 μ, and always evident on account of their slight affinity for stains. One or more vacuoles of non-colored matter, the paramitome of recent writers, may always be found, and in favorable cases there can be seen such a distribution of these as is shown in Figure 32. The *paramitome* exists in the form of numerous peripheral vacuoles subjacent to the enveloping connective fibres, and possibly (?) surrounded by them. The nucleus lies in a zone of clear matter, while the *mitome*, or filar substance, appears densest external to this. Between these and the first sort of ganglionic elements there exists every possible transition, so that this class is but poorly marked off from the preceding one. The vast majority of these cells are, however, of approximately uniform size, and I therefore cannot agree with Nansen ('87, *note*, pp. 113, 114) when he maintains that such transitional forms forbid the grouping of these cells in different classes. Such intermediate forms serve rather to explain the development of the one type from the other, without detracting from the individuality of either class.

The third type is that of the large[1] cells, represented in Figure 2 Plate III. These vary considerably in size and shape ; the mean long tudinal diameter is 55 μ, the transverse 40 μ. The cell protoplas stains rather deeply, and is notably granular. These granules resol themselves in the nerve processes into fine lines. Each large ganglion cell contains a number of clear spaces, the paramitome, exactly simil to those already described for cells of the second class ; and these a often arranged concentrically, and more or less regularly along tl periphery of the cell. The single nucleus, 15 by 12 μ in diameter, usually found nearer the end of the cell from which the nerve fib emerges, and, in contrast with those already described, is stained on lightly. A nuclear membrane is very distinct, and there is one lar nucleolus 2–3 μ in diameter. In rare cases two smaller nucleoli we found, never more. The nucleus also contains numerous fine granul of chromatine, which are very distinct in the matrix, which remai completely unstained. Nuclei of this class are not infrequently cre centic, with a clear space enclosed by the horns of the crescent, corr sponding exactly to such forms as are figured by Rhode ('87, Taf. I Fig. 51 *et al.*). Although variable, these cells represent a more isolat type than either of the other classes, and intermediate forms, especial in nuclear appearance and structure, are rarely seen in the brain.

An examination of the ventral nerve cord in transverse section sho a preponderance of cells of the second class. The first class is poor represented, though the size of the plasmatic portion varies greatly different cells. Occasionally one finds cells which in their deep staini and nuclear appearance recall the large cells of the brain. But mea urements showed one such cell to be only 24 by 30 μ and its nucle 7 by 11 μ in diameter, dimensions which are far smaller than those the average of the large cells in the brain. These cells do not seem be regularly arranged in the ventral nerve cord, and no grouping cou be found which suggested metamerism. The peripheral nervous ple possess very few ganglionic elements, and these few are not reducible the types present in the central nervous system, for they are invariab multipolar, and are situated at the crossing or branching of fibres.

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[1] It is much better, for the sake of clearness in neurological terminology, keep the term "giant cells" (Riesenzellen) for the huge elements in the n vous system of Nemertines, Annelids, *et al.*, as German writers have done, tha with Shipley ('90, p. 16) and Andrews ('90, p. 424), to apply the term to su cells as I have placed in the third class, to which the former are at most only r motely homologous.

The *internal structure of the brain* shows a strictly bilateral arrangement of the elements. A transverse section through the middle of the ganglionic mass is represented in Figure 24 (Plate III.). The fibrous matter is collected into two commissural masses, in which the fibres run both anteroposteriad, chiefly at the lateral extremities, and laterally, chiefly in the middle. The real relation of these commissures to each other is first seen in sagittal sections (Plate II. Figs. 19 and 20), where the fibrous matter has the form of a > with the apex directed forward. The dorsal arm of this > is prolonged backwards in two lateral horns, which are surrounded by ganglionic cells. The tips of these horns, cut transversely, are seen in Figure 25 (Plate III.). The similar ventral horns are the roots of the circumœsophageal connectives. From near the anterior apex of the > a small arm of fibrous matter is directed forward, as seen in a sagittal section of the brain near its left lateral margin (Plate II. Fig. 19). This becomes, in a median sagittal section, a small commissure cut transversely (*coms. a.*, Fig. 20), and separated from the brain by the connective-tissue capsule. This commissure is at its right side again connected with the brain, as already described, for the left extremity. Thus it resembles in its form and relation to the main fibrous mass of the brain the handle of a basket, the handle being directed forward. It lies, as can be easily seen from the figures, immediately below the surface of the cerebral organ, and its relation to that structure will be more fully explained later.

The arrangement of the ganglionic elements in the brain is somewhat definite. Ganglionic cells of the first sort are found in nearly every part, and make up all diffuse centres, where, however, transitional forms render their separation from the second class difficult. The former are most strongly marked at the tip of the dorsal horn (*cl. gn. I.*, Fig. 25), where they are very densely crowded. They cover also the lateral and dorso-lateral aspects of the dorsal commissure (Fig. 24) in similar dense masses. The anterior face of the fibrous matter is also almost exclusively occupied by cells of the first class; and from this region they extend a short distance ventrally. Here one finds a gradual transition into the ganglionic cells of the second class (*cl. gn. II.*, Plate II. Fig. 20, Plate III. Fig. 24), which occupy the entire ventral and posterior aspects of the fibrous matter. These cells also fill the space between the dorsal and ventral commissures, but are found dorsally only between the two lateral fibrous swellings on the lateral edges of the dorsal commissure. They are never so crowded as cells of the first class, and display no particular arrangement into clusters or groups.

The large ganglion cells of the third class (*cl. gn. III.*) are present in a somewhat limited number, and always in a definite position. They lie in the posterior third of the brain, on its medial posterior boundary (Figs. 19, 20, 25). The large fibres which pass off from these cells are easily seen to turn toward the opposite side of the body and to make their way into the ventral commissure, where they are lost to view, either because they are split up into a number of small ones, or from some other cause suffer a diminution in diameter. This crossing of fibres from cells on one side of the body to the connective[1] of the other certainly does not take place frequently in either of the other two groups of ganglionic cells. Wherever circumstances permitted the following of nervous processes in groups I. and II., these were seen to pass off towards the connective on the same side of the body as the cell itself.

b. Cerebral Nerves.

From either side of the brain two groups of nerves pass off; the anterior consists simply of the first tentacular nerve (*n. ta. 1,* Fig. 22, Plate II.); the posterior contains the second, third, and fourth tentacular nerves and the œsophageal connective. The tentacular nerves radiate from the brain to the aboral wall of the tentacular fold, and, splitting there into numérous branches, follow the aboral wall of the blood cavity toward the distal margin of the fold. The first tentacular nerve supplies that portion which was designated as the dorsal horn. Following the margin of the fold from this region toward the ventral line, its successive parts are seen to receive their nerve supply from the third, second, and fourth tentacular nerves successively. Each of these innervates about equal portions of the fold. I was unable to trace the ultimate termination of the nerves in this region.

The œsophageal connectives give off each three branches: (1) the splanchnic, (2) the muscular, and (3) the inferior muscular. The splanchnic is given off ventrally and medially immediately after the connective leaves the ganglion (*n. spl.*, Figs. 22, 25). It passes diagonally forward, — *not posteriad,*[2] *as stated by other writers,*[3] — and into the circular muscles of the pharynx, where it terminates in a distinct ring at about the level of the middle of the brain.

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[1] I use the word *connective* in the sense first suggested by Lacaze-Duthiers, to distinguish the nerve fibres joining ganglionic nerve centres which are on the same side of the body, reserving the word *commissure* for such fibres as cross the median plane of the body.

[2] This nerve is turned backward in Figure 22, for the sake of clearness in the drawing. Normally, it extends forward *under* the ganglion.

[3] This relation is obscured when the introvert is slightly retracted, and even apparently reversed when the retraction is greater.

At the point where the splanchnic nerve forms a ring around the pharynx one finds a few nerve cells, but they are few in number, and hardly deserve the name of a ganglion. From this ring it is easy to trace in serial sections the stems of the intestinal plexus, which are here large. This plexus lies in the connective tissue of the intestinal wall, and was first described by Andrews ('90, p. 405) for S. Gouldii. However, he failed to find a splanchnic ring, or any anterior connection of the plexus with the central nervous system.

The muscular branch (*n. mu. ret.*) passes off laterally from the middle of the œsophageal connective, and divides near the centre of the fused mass of the dorsal and ventral retractors into two branches, one of which traverses each retractor. Not far behind this branch there is upon the connective a small trunk (*, Fig. 22), which passes to the surface of the muscular mass, but which could not be traced farther. It remained doubtful whether this was a subsidiary muscular branch or of other value.

c. *Ventral Nerve Cord and Plexi.*

After the union of the two connectives, the ventral nerve cord thus formed floats a short distance free in the body cavity, and sends off numerous long nerves to the body wall. The first of these, the composite nerve of Andreae ('81, p. 248), is by no means always composed of eight branches in a single sheath, as stated by that author. The number varies from six to nine, and the size of the different trunks varies as well (Plate II. Fig. 22, *I.*). In fact, the later branches, which according to him consist of two trunks, one from each side of the nerve cord, not only show great variability in the size of these trunks (Fig. 22, *II.*), but also at times only a single trunk can be found, which then comes from but one side of the nerve cord. All these frequent irregularities point to a lack of metamerism in the nervous system. On reaching the body wall these nerves branch in a digitate manner through the muscles of the introvert, the main trunks being longitudinal, and do not form nervous rings around the body as in other parts of the wall. From these longitudinal stems large trunks pass outward through the musculature to the dermal plexus.

This dermal plexus lies in the cutis at its plane of union with the musculature, and consists of large longitudinal trunks (*plx. n. drm.*, Plate I. Fig. 4) with lateral anastomoses. From this network, fibres (*rm. gl.*)

pass outward through the cutis to the multicellular glands and to the hypodermal cells, as already described, as well as inward (*rm. mu.*) to the muscles. The existence of such a plexus has already been shown by Andrews ('90, p. 395) for S. Gouldii. To his description, which answers equally well for S. nudus, I can only add a few observations as to the histology of the nerve trunks. Each of these possesses a well defined sheath or neuroglia (*n'gl.*, Fig. 5), in which discoid nuclei (*n'gl. nl.*) measuring 2 by 4.5 by 6 μ are common. These nuclei lie either inside or outside of the membrane; they may be stained deeply, and contain many nucleoli. The substance inside the neuroglia has a distinct fibrillar appearance, and when these nerve stems were bent upon themselves so as to be cut transversely and still extend longitudinally within the same section, the fibrillæ appear in the transverse section as dots. These are also the fibres which are connected with the cells of the multicellular glands (*gl.‴ n. fbr.*, Plate I. Fig. 14).

The existence of the peritoneal plexus found by Andrews ('90, p. 395) in S. Gouldii could not be demonstrated in preserved specimens. No doubt the examination of fresh material will show its presence in S. nudus as well.

4. Cerebral Organ.

This interesting structure may be considered under two heads: first, the canal; and secondly, the surface next to the brain, or the cerebral organ proper.

The canal opens, as already described, on the dorsal median line, just posterior to the tentacular fold (*can. o. ceb.*, Figs. 2 and 3). From this point it extends posteriad about 1.5 to 2 mm., to the anterior ventral surface of the brain, where it terminates blindly (*o. ceb.*, Fig. 3). From the marginal fold which surrounds the opening arise numerous longitudinal ridges, which traverse the entire canal, and give it in transverse section (*can. o. ceb.*, Plate III. Fig. 26) a branched appearance. In a surface view the walls of the canal appear thickly spotted with brown, and further examination shows this to be due to the presence of large numbers of the characteristic pigment cells, which are usually seen crowded in masses along the summits of the ridges (*cl. pig.*, Fig. 26). It is probably this canal which was found by Keferstein und Ehlers ('61, p. 47) in S. tesselatus. The canal is correctly figured (Taf. VII. Fig. 1, 2, *u*, *u'*), but they evidently mistook its true character, since they say: "Ausserdem sieht man vom Hirn zum Tentakelkranz *einen aus zwei Hälften bestehenden, dicken Strang* verlaufen, der dort endet, und an dem Endpunkte, wie man bei der Betrachtung von aussen her wahrnimmt, in der Haut von einer Gruppe kleiner Falten umgeben ist als wenn er *eine Röhre wäre* und hier nach aussen mündete."[1] Among recent writers, Vogt und Yung ('88, p. 404) mention and figure the "cerebral canal," without a more particular description of its structure or morphological relations.[2]

The histological study of the canal shows some features of interest. Its entire surface is lined by an extremely thin cuticula, which appears under high powers merely as a double contour, pierced by numerous short cilia. The cells of the ventral wall of the canal have the appearance of ordinary hypodermal cells, except that they bear cilia. The dorsal wall is made up of similar cells near the mouth of the canal, but these become higher as the brain is neared, until at the middle of the canal they have assumed the form of a high columnar epithelium with large nuclei. This condition is preserved up to the surface of the brain. When examined more closely, these cells are seen to be filled with granules of a highly refractive nature, especially at their distal ends, and may be regarded as the source of the more or less extensive coagulum always found at the basal end of the canal. We have here, then, the secretive portion of this organ.

In cross sections of the canal (Plate III. Fig. 26) one sees clearly a group of muscular fibres which is deflected from the circular layer of the body wall and encircles the canal in the form of a sphincter (*spht.*), which, although most marked at the opening of the canal, is present along its entire extent. The function is evidently to prohibit the entrance of extraneous matter during the forward motion of the animal, and to assist in changing the water contained in the canal. In the latter function it would be assisted by the cilia lining the canal.

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[1] The Italics are not in the original.

[2] P. S. — Since writing the above, I have obtained access to a preliminary communication by Spengel ('77), and find that in this he has maintained "die Existenz eines vom Gehirn zur Basis der Tentakeln führenden, offenen Canales." Spengel was thus the first to arrive at the true form of this structure, but I cannot find that he has anywhere given a more detailed account of its morphological or physiological character. In the same paper he says: "Das Gehirn stellt sich als eine knopfartige Verdickung des diesen Canal auskleidenden, mit der Epidermis zusammenhängenden Epitheles dar." Against this interpretation it may be said that the embryological evidence of Hatschek ('83) makes it probable that the canal is secondarily formed. Furthermore, a histological examination of the parts shows that the brain is less closely connected with the cerebral organ than appears superficially, since the brain capsule separates the two completely, except at the entrance of the anterior commissure, which furnishes the nervous supply to the organ in question. A full discussion of these relations follows the histological description of the cerebral organ which is given later.

At its posterior end the canal widens abruptly into a saucer-shaped cavity, which lies with its concave surface upon the antero-ventral face of the brain (Figs. 3, 20, 27), and includes a low rounded prominence (*o. ceb.*) which I regard as the cerebral organ proper. Macroscopically, this appears to be continuous with the brain, but internally the connective-tissue capsule separates it almost entirely from the ganglionic mass. The histological character of this prominence, and its relation to the brain, require more extended consideration.

When one examines a longitudinal section of this region (Plate III. Fig. 27), perhaps the most striking feature is the extremely prominent cuticula (4 μ in thickness), which covers exactly the convex surface, and only that portion, for at the margin of this convexity (†, Fig. 27) it passes abruptly over into the very thin cuticula of the canal wall. At each *lateral* edge of the cavity there is a considerable thickening of the cuticula, which extends a short distance into the subjacent tissue and has in cross section the outline of a small retort. The cuticula presents a sharp outer boundary, and there one finds no remnants of cilia in the sections, yet I am inclined to think that cilia are present in the living animal. For in preserved specimens the entire lower portion of this canal is filled with a granular coagulum, which might easily enclose and obliterate cilia, if indeed any were preserved in this deep and narrow canal, where fluids evidently could not readily penetrate. The lateral cilia, which are perfectly distinct in the anterior half of the canal, become gradually less so, until in the lower portion, which is filled with this coagulum, they entirely disappear. In partly macerated specimens this thick cuticula breaks up into small blocks along lines extending perpendicularly to the surface, so that one may reasonably assume that there is a ciliated condition of this surface in the living animal.

It is difficult to study the cells which underlie this cuticula, inasmuch as the cell boundaries are very indistinct; the most evident feature is the regular row of nuclei which lies close under the cuticula. From these a crowded mass of nuclei (*cl. gn.* ?) and fibres extend at right angles to the surface into an irregular group of fibres (transsected in Fig. 27, *coms. a.*), — the anterior commissure already described. If one examines the nuclei, their resemblance in size, shape, and optical properties to those of the central nervous system is evident. An actual entrance of the fibres into this anterior commissure can also be easily observed. The connection of these fibres and nuclei with the hypodermal

lls is very difficult to prove in sections; but in a badly preserved and
nce partially macerated preparation there was in many places a defi-
te continuity of these cells with the fibres and underlying nuclei.
e probability of a direct continuity of the hypodermal cells with the
ntral nervous system through the anterior commissure seems to me to
strong evidence in favor of the special sensory nature of the organ.
n examination of its morphological relations also yields much that is
vorable to this view.

The existence of a glandular area, the direct connection of the organ
th the central nervous system, and its median position near the an-
rior extremity of the body, all point to its close relationship to such
nse organs as are cited by Dewoletzky ('87, p. 278), and as are com-
on in the class Vermes. These have their origin, according to Dewo-
zky, in "ein Paar flimmernder Hauteinstülpungen." Whether the
me holds for this cerebral organ of Sipunculus can naturally be de-
led only upon embryological evidence. Hatschek ('83, p. 115) says
at toward the close of the larval stage two "Wimpergruben" are
rmed, one on either side of and near the median line. Further, he
ys, "Es sind dies wohl Sinnesorgane die sich wahrscheinlich auch am
wachsenen Thiere werden nachweisen lassen." These would by their
sion produce an organ which, in position at least, would correspond
that which I have described; and from the absence of any other
ructure to which these Wimpergruben can be traced, it is allowable
assume their genetic connection with this cerebral organ until the
velopment shall furnish positive evidence on the question. That this
gan might be the apical area (Scheitelfeld) which, by the recession of
e brain from the surface, had come to be connected with the exterior
means of a canal, is disproved by Hatschek's ('83, p. 108) observa-
on that there is a complete separation of the ganglion from the body
ll at the time of its retreat; according to the same author, the forma-
on of the Wimpergruben was subsequent to this separation.

If, now, the other members of the group of Sipunculids be examined
r similar structures, two cases are found which require consideration.
ipley ('90, p. 18) has described an infolding of the preoral lobe which
tends to the surface of the brain, and from which a pair of retort-
aped tubes penetrate into the ganglionic mass, one at each dorsal
eral angle of the brain. The cells of the inner limb of the tubes
crete a black pigment. Andrews ('90, p. 418) finds in S. Gouldii two
nilar tubes proceeding from the lateral edges of a transverse pit an-
rior to the ridges of the ciliated cushion. These tubes extend into

the ganglionic mass, and contain a coagulum, but have no pigment. Comparing these two accounts with each other and with that just given of the cerebral organ in S. nudus, it will be seen that the tubes lack pigment in S. Gouldii, and that both tubes and pigment are wanting in S. nudus, unless the regions of thickening in the cuticula on the lateral aspect of the cerebral organ noted above be the rudiments of such structures. The optic nature claimed by Shipley for the tubes in Phymosoma agrees with their reduction or disappearance in the forms inhabiting the sand. The position of the organs would seem to indicate an homology between the ciliated cushion of S. Gouldii, the deep pit of the preoral lobe in Phymosoma, and the cerebral organ in S. nudus. As to the histological character of the organ in Phymosoma, nothing is found in the account of Shipley. Andrews describes that of S. Gouldii as ciliated and well supplied with nerves. The deep location of the organ in S. nudus may be merely for protection, or perhaps due to the development of the glandular area, or even necessitated by the recession of the brain from the surface. The canal is much longer in S. tesselatus, where the brain also lies deeper in the body, than in S. nudus. An analogous variation may be seen in the deep-seated lateral organs of the Enopla as compared with those of the Anopla.

Finally, if it be asked why the whole structure may not be regarded as a degenerate organ, of which the pigmented tubes were originally the active portion, I can only say that the active glandular area and ciliated canal cannot be explained on such an assumption, and still less can the special nervous supply. I studied the structure a long time with this idea in mind, but finally became convinced that it was untenable in every respect. Although the evidence is far from complete, I regard it as an actively functional organ, morphologically the equivalent of the ciliated cushion of Phascolosomes, and possibly with a more highly specialized function, since it certainly has a more highly differentiated form.

Such organs are by no means rare. Dewoletzky ('87, p. 277) has given a list of similar ones, and has considered at length their probable function, which he regards as "some sort of general perception as to the character of the surrounding medium."

IV. Conclusions.

If now the account I have given of certain points in the anatomy and histology of S. nudus be compared with that given by Andrews ('90) for S. Gouldii, it will be noticed that, while there is a general similarity, a correspondence in details is wanting. The dermal glands are hardly more than similar in type, and a direct correspondence between the different kinds is not to be found ; for the bicellular are entirely wanting in S. Gouldii, and the multicellular of S. nudus agree with neither group described for S. Gouldii. Whether the non-glandular organs of Andrews correspond to the small papillæ described above cannot be lefinitely determined, on account of the brevity of Andrews's description and the lack of figures. On the other hand, Andrews has emphasized he fact that a close agreement exists between the dermal bodies of S. Gouldii and those of various Phascolosomes. Again, in the arrangenent of the musculature, in the uniform unbanded circular layer, in he absence of diagonal fibres, and in numerous other details, S. Gouldii s unlike S. nudus, and in the same degree that the former resembles Phascolosoma. In the light of these facts, a modification of the generic haracters given by Selenka ('83) to Sipunculus, which include S. Gouldii n the same genus with S. nudus, would seem advisable.

Striking as is the similarity between the anatomy of the nervous sysem in the Annelids and in the Sipunculids, certain characteristic diferences are worthy of note. The peripheral system of plexuses is very highly developed in the latter, and consists almost entirely of ibres, whereas the dermal plexus of Capitellids, Nemertines, and Polyhæts is composed largely of ganglionic cells. In the ventral nerve ord of Sipunculids there is no metameric arrangement of the lateral ranches, nor any concentrations of the ganglionic elements in the cord tself. On the other hand, there is present a splanchnic nerve and an ntestinal plexus in both Sipunculids and Annulata, and the complicated tructure of the supracesophageal ganglion in Sipunculus agrees in genral with that of various Annelids and Nemertines.

As regards the histology of the central nervous system, it will be oticed that the description given in this paper for S. nudus corresponds losely with that given by Rohde ('87) for Chætopods, and by Bürger '90) for Nemertines. It is of interest, however, to note more exactly he points of likeness and difference. If further investigation should lead o the discovery of a minimal cell body for the nervous nuclei (Nervenerne) of Rohde, — and I think this probable on account of the extreme ifficulty experienced by Bürger ('90, p. 106) and myself in finding this ell substance, — then these nervous nuclei would correspond in general haracter and occurrence with the first class of ganglionic cells described y Bürger in Nemertines, and with the first type in Sipunculus. The rst class of Rohde agrees in general with the second of Bürger ; but both differ from the second type in Sipunculus in one important poin namely, their arrangement. While they are (always?) found groupe in clusters in the brains of Polychæts and Nemertines, such an arrangement is never unquestionably present in Sipunculus, though indication of a regular grouping were sometimes noticed. This may be regarded perhaps, as indicating a less highly specialized condition in the Sipunculid nervous system. According to Rohde and Bürger, these cells hav nuclei slightly smaller and more deeply stained than those of the firs class. I did not find any such difference between the two groups i Sipunculus. The third type of cells in the Sipunculid brain show also a general correspondence to Class III. of the Nemertines an Class II. of the Chætopods. In both Chætopods and Nemertines ther exists a fourth type, — the paired "giant cells" of the central nervou system, with their accompanying "giant fibres." These are entirel lacking in the Sipunculids. No one of the large cells has acquired an uniform or considerable superiority of size over its fellows. Furthermore no giant fibres can be found in the ventral nerve cord, so that thes elements probably do not exist in the Sipunculid nervous system. This may be regarded as further proof of the lower grade of specialization i the Sipunculids.

The earlier investigators regarded these "giant cells" as "Bildungen ganz verschiedener Art" (Spengel, '81, p. 40), but the more recent writers incline toward the opinion that they are homologous throughout (Eisig, '87, and Friedländer, '89). Now, either these "giant cells" are neomorphic in both groups, and hence not at all homologous, or the Sipunculids were separated from the primitive stem before the separation of Nemertines and Annelids took place, and before the differentiation of these elements had been effected. A complete disappearance of giant cells and giant fibres in the Sipunculids is hardly probable, in the light of the persistence of these and all other nervous structures. This would put the origin of the Sipunculids farther back than has usually been maintained, and would make their relationship to the Annelids somewhat distant. Of importance in this connection is the simple undifferentiated condition of the ventral nerve cord, which shows no trace of a metameric concentration of ganglionic cells, such as is found in the Annelids. According to the researches of Andrews ('90), moreover, the lateral branches lack that metameric character which has heretofore been assigned to them, and I have been able to confirm this in part for S. nudus. Lack of metamerism in the adult, as well as in the larva, would serve to strengthen the view of only a remote relationship between Annelids and Sipunculids, as has long been maintained by Hatschek ('80 and '83) on embryological grounds.

The existence of at least giant fibres has been proved for Echiurus by the researches of Greeff ('79) and Spengel ('80, p. 487), and more recently for Thalassema by Rietsch ('86, p. 402), so that the presence of corresponding ganglionic cells may be reasonably assumed. This is, then, a further ground for separating the Sipunculids from the Echiurids, and for assigning to the latter a closer relationship to the Annelids than the former have. This position has been defended from an embryological standpoint by Hatschek ('80, p. 71) and Conn ('86, p. 399).

In spite of the well known conservatism of the nervous system, I am well aware of the dangers of such conclusions based upon the study of a single system or a single form. The foregoing comparison is offered, then, merely as a new side light on the unsettled question of the position of the Sipunculids, and in the hope that the accumulation of evidence from various sources may some day bring a clear and full solution of the problem.

January 20, 1891.

Addendum.

During the correction of the proof-sheets there has appeared a second paper by Shipley ('91) on Phymosoma (P. Weldonii, *n. s.*). It is interesting to note that the gland cells there described (p. 114) correspond very closely to the multicellular glands of S. nudus, except that no connection with nerve fibres is reported. Shipley affirms positively (p. 115) "the absence of those skeletal cells which formed so interesting a feature" of P. varians (Shipley, '90, p. 9). That such a tissue does not exist in S. nudus has already been emphasized. This is then strong proof that it is an individual peculiarity of the one species, rather than an ancestral relic. In general the claimed relationship of Sipunculids and Phoronis seems to me to have little in its favor beyond the external similarity of the two forms.

It is a pleasure to see that Shipley and I have both arrived independently at the same conclusions regarding the vascular system. He ('91, p. 116) does not regard it as important in respiration, and explains the cæcal diverticula of the dorsal vessel, which might be looked upon as strengthening the view of its respiratory nature, as merely reservoirs for the increased overflow from the tentacles, which are exceptionally numerous in this species.

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EXPLANATION OF FIGURES.

All figures were drawn with the aid of an Abbé camera, unless otherwise stated. They represent without exception preparations of *Sipunculus nudus*, L. The method of staining and systems employed are indicated briefly for each specimen.

ABBREVIATIONS.

can. o. ceb.	Canal of cerebral organ.
cl. gn. I., II., III.	Ganglionic cell I., II., or III.
cl. fil.	Filamentous hypoderm cell.
cl. pig.	Pigment cell.
cl. sns.	Sensory cell.
coms. a.	Anterior commissure of brain.
coms. d.	Dorsal “ “
coms. œ.	Œsophageal connective.
coms. v.	Ventral commissure of brain.
con't. tis.	Connective tissue.
cps. enc.	Capsule of brain.
crnu. d.	Dorsal horn of tentacular fold.
ct.	Cutis.
cta.	Cuticula.
gl.″	Bicellular gland.
gl.″ dt.	Duct of bicellular gland.
gl.″ env.	Envelope “ “
gl.″ nl.	Nucleus “ “
gl.″ vl.	Vacuole “ “
gl.‴	Multicellular gland.
gl.‴ dt.	Duct of multicellular gland.
gl.‴ env.	Envelope “ “
gl.‴ n. fbr.′	Nervous fibrilla to multicellular gland.
gl.‴ nl.	Nucleus of the multicellular gland.
gn. su'œ.	Supraœsophageal ganglion.
h'drm.	Hypodermis.
leu'cy.	Leucocytes.
mb. ba.	Basement membrane.
mit.	Mitome.
mu. crc.	Circular muscles.
n'gl.	Neuroglia.
n'gl. nl.	Neuroglia nucleus.
n. mu. ret.	Nerve of retractors.
nl. sns.	Nucleus of sensory cell.
n. spl.	Splanchnic nerve.
n. ta.	Tentacular nerve.
o. ceb.	Cerebral organ.
or.	Mouth.
pa'mit.	Paramitome.
pap.	Papilla.
pli. ta.	Tentacular fold.
plx. n. drm.	Dermal nerve plexus.
pr'c. dg.	Digitate processes of brain.
rm. gl.	Glandular branch of plexus
rm. mu.	Muscular “ “
spht.	Sphincter of cerebral canal.
va. sng. d.	Dorsal blood-vessel.
va. sng. v.	Ventral blood-vessel.
z. lev.	Smooth zone of introvert.
z. pap. a.	Anterior papillate zone of introvert.
z. pap. p.	Posterior papillate zone of introvert.

PLATE I.

Fig. 1. Anterior half of the introvert. The base of the figure corresponds to the middle of the posterior papillate zone. The slight contraction at the centre of the zona levis is not usually found. Camera outline. Simple microscope. × 3.
" 2. Anterior aspect of tentacular fold. The figure is diagrammatic only to the extent that secondary folds are omitted. Camera outline. Simple microscope. × 4.
" 3. Sagittal section of introvert. Diagrammatic in regard to details. Simple microscope. × 8.
" 4. Longitudinal section of body wall of introvert in the anterior portion of the posterior papillate zone. Muscles diagrammatic. Böhmer's hæmatoxylin. Zeiss 3. A. × 98.
" 5. Transverse section of body wall at about the region indicated by the line *gl.″* in Fig. 4. Hamann's carmine. Zeiss 1. D. × 370.
" 6–8. Sections of bicellular glands in the three dimensions of space. Kleinenberg's hæmatoxylin. Zeiss apochr. 4 mm. Oc. 6. × 425.
" 6. Soon after the beginning of secretion. The membrane dividing the two cells is shown at *.
" 7. At the period of greatest activity in secretion.
" 8. At the close of secretive activity.
" 9. Transverse section of duct of bicellular gland immediately below the cuticula. Zeiss apochr. 4 mm. Oc. 6. × 425.
" 10, 11. Longitudinal and transverse sections of bicellular glands to demonstrate position of nuclei. Hamann's carmine. Zeiss apochr. 4 mm. Oc. 6. × 425.
" 12–14. Multicellular glands. Zeiss apochr. 4 mm. Oc. 6. × 400.
" 12. Longitudinal section. The duct is filled with a secreted material. Kleinenberg's hæmatoxylin.
" 13. Transverse section. At the left centre of the section a cell has fallen out. Hamann's carmine.
" 14. Longitudinal section to demonstrate nuclei and connection of gland cells with nerve fibres. Mayer's cochineal.

WARD.— SIPUNCULUS. PL. I

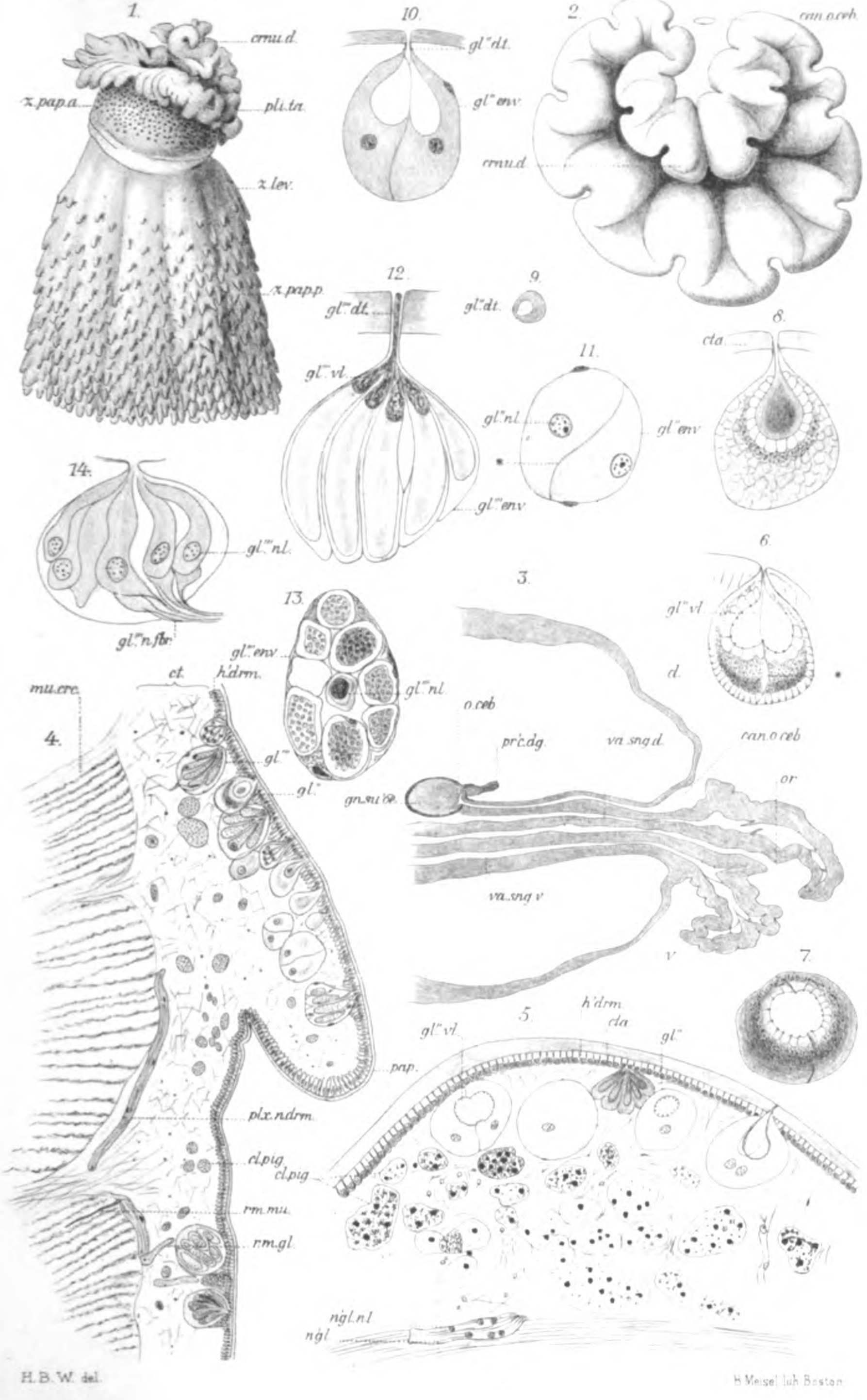

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PLATE II.

Fig. 15. Transverse section of epithelium of tentacular fold to show the leucocyte *in situ*. Hamann's carmine. Zeiss 1. E. × 500.

" 16–18. Sense papillæ from anterior papillate zone of introvert.

" 16. Tangential section through a single papilla. Hamann's carmine. Zeis 1. D. × 300.

" 17. Transverse section. Apical area retracted. Hamann's carmine. Zeis 1. D. × 330.

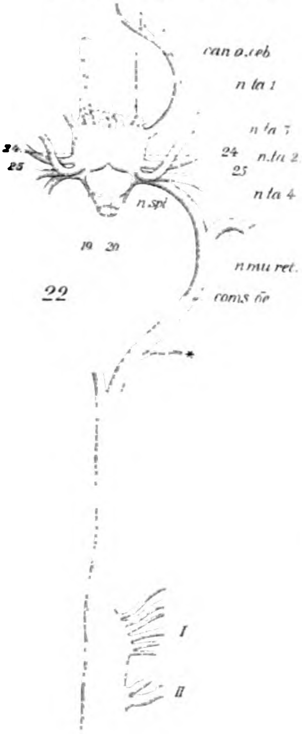
" 18. Transverse section. Papilla fully expanded. Orth's picro-litho-carmine Zeiss 1. D. × 220.

" 19. Lateral sagittal section of brain at point of departure of the anterior commissure from the central fibrous mass. Plane of section indicated o Figure 22 by dotted line "19." Mayer's cochineal. Zeiss 1. A. × 50

" 20. Median sagittal section of brain. Plane of section indicated on Figur 22. Mayer's cochineal. Zeiss 1. A. × 50.

" 21. Cells of tentacular epithelium isolated by maceration; *a*, *c*, and *e*, sensory *b*, *d*, and *f*, filamentous cells. Zeiss apochr. 4 mm. Oc. 8. × 725.

" 22. Central nervous system. Composite figure from maceration preparation controlled by serial sections. The splanchnic nerve (*n. spl.*) shoul project *forward* under the brain. For the sake of clearness it is represented as if turned posteriad; * denotes inferior muscular branch (?) The numbers denote the planes of sections represented in Figures 19 20, 24, and 25. × 8 (about).



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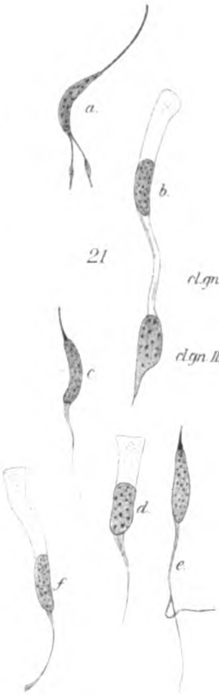

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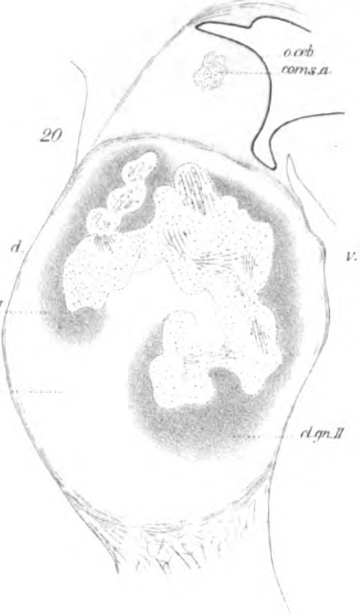

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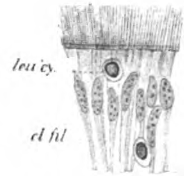

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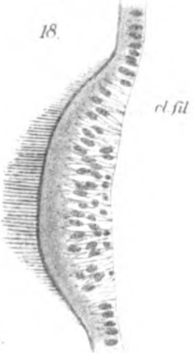

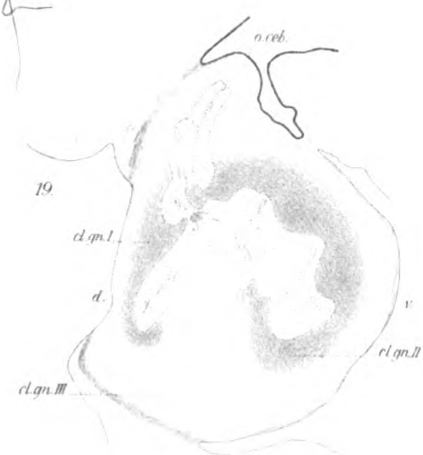

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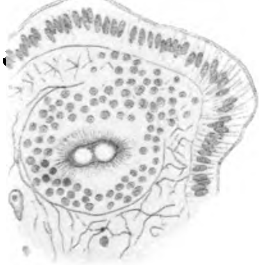

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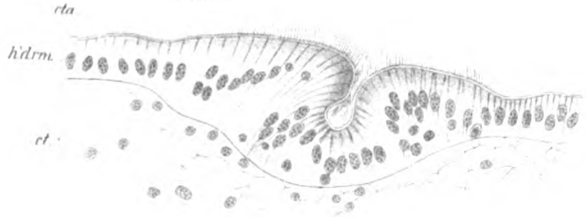


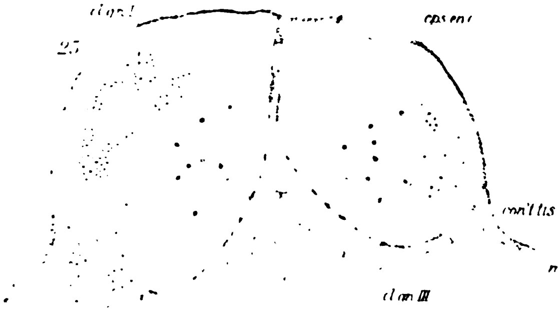
[illegible] W. del.

B. Meisel lith. Boston.

PLATE III.

Fig. 23. Transverse section of hypodermis of tentacular fold with sensory cell
Weigert's picro-carmine. Zeiss apochr. 4 mm. Oc. 8. × 725.
" 24. Transverse section of brain. Plane of section shown in Figure 22, Plat
II Grenacher's alcoholic borax carmine. Zeiss 1. A, × 50.
" 25. Transverse section of brain. Plane of section shown in Figure 22, Plat
II. The section was cut somewhat obliquely, and the right half lie
posteriad. Grenacher's alcoholic borax carmine. Zeiss 1. A. × 50.
" 26. Transverse section of body wall passing through the canal of the cer
bral organ at about the middle of its course. The left of the figu
is dorsal. Hamann's carmine. Zeiss 1. A. × 50.
" 27. Transverse section of the cerebral organ: only one half is represente
and but a small section is drawn in detail. The cerebral canal begi
at the angle near the number 27, and extends forward at right angles t
the surface marked *cta*. The transition from the cuticula of the cer
bral organ to that of the canal is marked by a †. Czokor's cochine
and picric acid. Zeiss apochr. 4 mm. Oc. 8. × 510.
" 28–31. Ganglionic cells. Zeiss apochr. 4 mm. Oc. 8. × 510. Fig. 28, Clas
III. Fig. 29, Class II. Fig. 30, Nuclei of Class I. Fig. 31, Class
" 32. Oblique section through a ganglionic cell of Class II., showing th
regular arrangement of the paramitone. Hamann's carmine. Zeis
apochr. 4 mm. Oc. 8. × 725.

23



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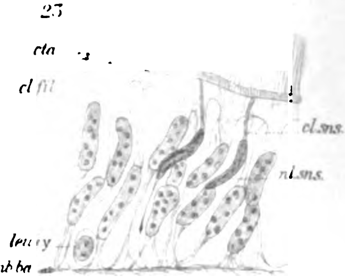

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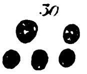

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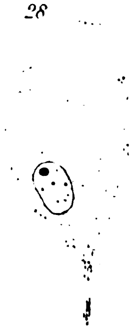

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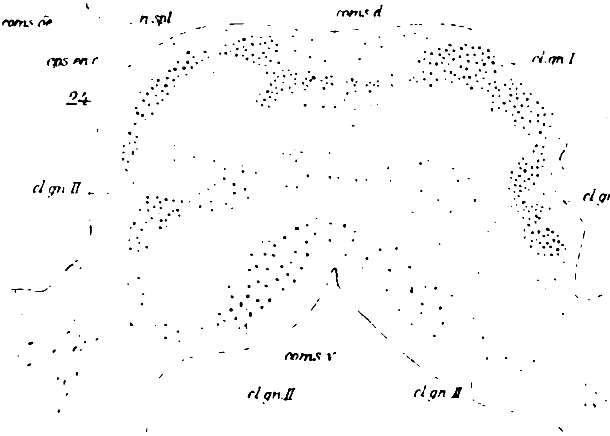

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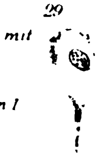

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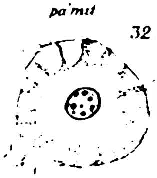

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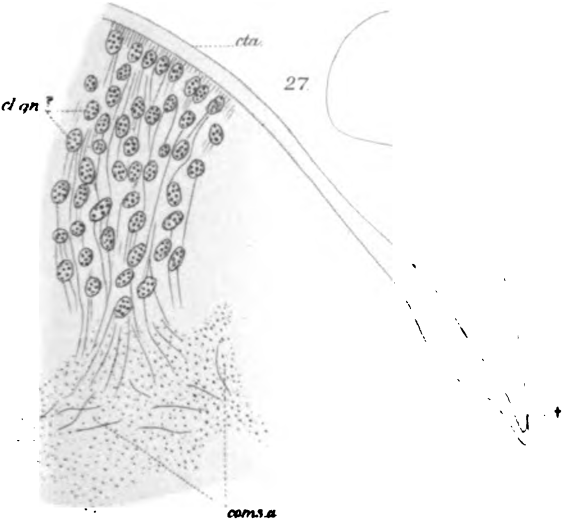

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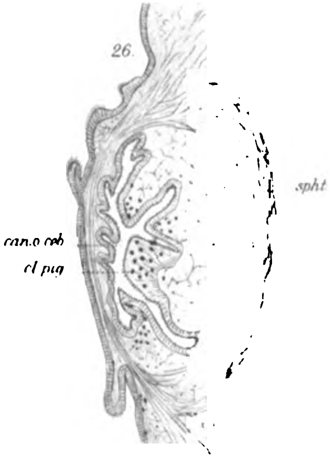

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E. Meisel lith Boston

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Bulletin of the Museum of Comparative Zoölogy,
AT HARVARD COLLEGE.
VOL. XXI. No. 5.

27

THE DEVELOPMENT OF THE PRONEPHROS AND SEGMENTAL DUCT IN AMPHIBIA.

BY HERBERT H. FIELD.

WITH EIGHT PLATES.

AM. ENT. SOC.

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I. Introduction.

The studies upon which this paper is based were undertaken with the purpose of determining the relation which the urogenital system bears to the germinal layers in Amphibia. At the time when they were begun, especial interest in this topic had been awakened by the appearance of Flemming's paper ('86), in which the author entirely confirmed the statement previously made by Graf Spee ('84), that the system was of ectodermal origin. This view was gladly welcomed on many sides, for it was felt that an origin from this source was more in harmony with general conclusions already accepted than was the method previously advocated. Moreover, a new light seemed now to be cast on the phylogeny of Vertebrates. Under these circumstances, it appeared highly desirable that the position which Graf Spee and Flemming had taken be subjected to the test of renewed investigation on other groups of Vertebrates than those employed by them. The researches of these authors had be conducted on Mammalian material only, and it was the hope of the writ to find in Amphibia a similar mode of origin for the excretory duct.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVII.

The material employed in the present investigations consisted of e bryos of Rana, Bufo, and Amblystoma. The study of the problem w begun with Rana pipiens Schreb. (halecina), embryos of which had be prepared in the spring of 1884 by Prof. E. L. Mark, who kindly plac his series at my disposal. In the spring of 1889, while in Baltimo Md., I secured an abundance of the eggs of Rana sylvatica Le Cont These eggs are large, measuring at the blastula stage two millimeters more in diameter. I also found them far better for embryological stu than those of other species of frogs examined. An advantage whi they possess for my purpose is that the germ layers are very well se rated from one another. Moreover, the body cavity appears at an ea stage, making the boundary between the somatic and the splanch mesoderm very pronounced, both in the region of the protovertebræ a of the lateral plates.

The eggs of Bufo studied, B. americanus Le Conte, were collected d ing the spring of 1887, in Cambridge and in Jamaica Plain, Mass. this time I also collected a small quantity of Amblystoma eggs fro pond in Jamaica Plain; but a careful search, carried on during seve subsequent trips to this locality, failed to yield any more eggs.

Prof. J. S. Kingsley at this time kindly sent me from Indiana so Amblystoma material which he had preserved; but for the determi tion of many points at issue I was obliged to wait till another seas offered opportunities for collection. In the spring of 1889, therefore made a trip to Baltimore, where I was able to collect an abundant s ply of the eggs of this Amphibian, most if not all of the material c lected belonging to the species A. punctatum Linn. In this work I w accommodated at the Biological Laboratory of the Johns Hopkins U versity, — a privilege for which I am under obligation to that insti tion. My thanks are particularly due my friend Dr. T. H. Morgan his kind assistance during my stay in Baltimore, and for material of collection.

I may here also express my obligations to Dr. John S. Billings, S

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[1] Inasmuch as the observations of European investigators have usually b made on R. temporaria, it is of interest to note that R. sylvatica Le Conte has b regarded by some systematists as a variety of R. temporaria (Günther, '58, p. In any event, the development of the two forms may be assumed to be v similar.

geon U. S. Army, for the favor of sending me from the Surgeon General's library in Washington a number of papers to which I should otherwise have been unable to gain access. I am further indebted to Mr. Samuel Garman and to Mr. G. H. Parker for the revision of my proof-sheets, and for suggestions during the progress of my work. Mr. Parker also read the earlier portions of my manuscript.

The material was prepared by ordinary histological methods; but inasmuch as many of the hardening reagents and stains which I tried gave thoroughly unsatisfactory results, I may state in brief the treatment which proved most successful. The embryos of both Rana and Bufo can be satisfactorily killed in Kleinenberg's picrosulphuric mixture; they can then be successfully stained in Orth's lithium-picrocarmin. The object should be exposed to the action of the stain as long as possible, care being taken to guard against maceration. In order to accomplish this purpose, it has frequently proved advantageous to stain the object twice, removing it after the first staining to strong alcohol. In passing the stained object through grades of alcohol, it is important to keep a little picric acid dissolved in the several fluids in order to prevent the alcohol from extracting the yellow stain from the specimen. Embryos treated in this way show a very effective double stain. The nuclei are bright carmine, contrasting with the yellow color imparted by the picric acid to the yolk spherules among which they are found. As a killing reagent, Merkel's fluid also gives good results. It should be followed by Kleinenberg's hæmatoxylin, and the decolorizing should be watched with care.

With Amblystoma the best method of treatment is that with Fol's chromic-osmic-acetic mixture, followed by Czokor's cochineal. The picrosulphuric mixture followed by picrocarmin, as recommended for Rana and Bufo, is also of service.

It is usually best to stain on the slide; and, in my experience, satisfactory results with hæmatoxylin can very rarely be reached by staining *in toto*.

II. Descriptive Part.

In the following account of the development of the pronephros and segmental duct, I shall first treat these organs descriptively. For this purpose, I shall take up in succession Rana, Bufo, and Amblystoma, and shall describe selected stages in the development of each. This account will be followed by a general discussion of nephridial organs, in which the results of other investigators will be reviewed.

A. Rana.

Stage I.

Plate I. Figs. 1-3.

At the first stage which I shall describe the embryo has departed on a little from the spheroidal form presented by the egg during segment tion. The medullary plate is widely open, its lateral margins being on slightly elevated above the general surface. At the hinder end of t medullary plate the blastopore is plainly visible. An idea of the ext nal form of the embryo can be gained by reference to Goette's figure Bombinator ('75, Taf. III. Fig. 41), or to van Bambeke's of the Axol tyl ('80, Pl. XII. Fig. 9). In water of 15 to 18° C. eggs of R. sylvati reached this stage in about sixty hours after fertilization; the eggs R. halecina develop somewhat more slowly.

The general relations of the germinal layers at this stage are shown Figure 2. The ectoderm consists of two distinct layers (Figs. 3 and *ec'drm.'* and *ec'drm.''*). Except in the region of the medullary thicke ing (*la. med.*), which is produced by a proliferation of the deeper these two layers, the ectoderm is nearly uniform in thickness. The tw layers present slightly different histological characters. In the out layer (Figs. 3 and 7, *ec'drm.'*) the cells are large and columnar, and the external surfaces project as rounded eminences, giving a roughly granul appearance to the surface of the embryo. Each cell contains scatter pigment granules, which are especially massed along its external fac Small yolk spherules (*sph. vt.*) are present in considerable number The cells of the deep layer (*ec'drm.''*) are smaller than those of the oute and are somewhat flattened. The pigment granules are scattered throug out the cells of this layer, without showing special accumulations. Th yolk spherules present the same appearance as those of the superfici layer.

The entoderm and yolk cells (Fig. 2, *en'drm.* and *cl. vt.*) form the gre mass of the interior of the embryo. The wide lumen of the gut tra erses the dorsal portion of this mass. The chorda (*n'cd.*) has the for of a longitudinal ridge, imperfectly cut off from the entoderm below, ar in contact with the medullary plate above. A single cell layer (*en'drm* on each side of the chorda forms the dorsal roof of the intestine. A this layer passes out laterally, it increases in thickness, becomes sever cells deep, and finally merges in the mass of large yolk cells (*cl. vt.*) lyin ventral to the intestinal cavity. All the cells of the entoderm contai large yolk spherules. Pigment is present in considerable quantity in th cells bordering the cavity of the intestine; elsewhere it occurs only as scattered granules.

At this stage two plates of mesoderm (Fig. 2, *la. ms'drm.*) extend out laterally, one on each side of the chorda, and pass ventrally around the mass of yolk cells to be united in the median line below. Each plate is thickest (Figs. 1, 3, at *la. pr'vr.*) next the notochord; as it passes outward, it becomes thinner. Before the ventral surface of the embryo is reached, it is reduced to a layer two cells thick, representing the somatopleure and splanchnopleure (*so'plu.* and *spl'plu.*) of this region. The cells of the mesoderm are in general smaller than those of the yolk-entoderm. The yolk spherules which they contain are also somewhat smaller than those in the entoderm. Pigment is rarely present except in the form of scattered granules.

In the foregoing account of the relations of the germ layers the description refers in the main to the typical condition, realized in the middle trunk region; in this and in subsequent stages modifications occur in the head and tail regions. These special conditions are of no consequence for the present purpose.

There are certain histological characters, to which allusion has already been made, which may serve as criteria for distinguishing the germ layers. The most satisfactory of these is the size of the yolk spherules. As I have indicated, the spherules are largest in the entoderm and smallest in the ectoderm; in the mesoderm they are of an intermediate size. Measurements of spherules from the three layers in the region of the future pronephros gave the following results: entoderm, mean diameter of spherules, $8\,\mu$; mesoderm, mean diameter, $5\,\mu$; ectoderm, diameter rarely exceeds $3\,\mu$. Excluding the head and tail regions, these dimensions represent, I believe, fair averages for the whole body. The distribution of pigment affords another criterion for distinguishing the layers. In the superficial ectoderm, the pigment (Figs. 3, 7) is massed along the external surface of each cell. In the deep ectoderm, it is present in considerable quantity, but is scattered throughout the cell. Except in certain specialized regions, there is little pigment in either mesoderm or entoderm. I have also noted the differences in the mean sizes of the cells: the yolk cells are in general the largest, and those of the ectoderm the smallest, the mesodermal cells being of intermediate size. The great variability of this character prevents its having much weight, however, in determining to which of the three layers a given group of cells belongs.

I shall now consider in greater detail some of the modifications which

the mesoderm exhibits, particularly such as occur in the region wh
the pronephros is subsequently developed. For this purpose I ha
selected two embryos of Stage I. which show slightly different con
tions. The account will first relate to the specimen which is shown,
the less differentiation of the medullary plate as well as by other featu
to be the younger. This embryo measures 2.31 mm. in length. In f
lowing a series of cross sections forwards, the three germ layers beco
apparent at about 0.35 mm. from the posterior end, or a short distan
in front of the blastopore. Here the structure of the mesoderm is rath
obscure, since in a transverse section of the animal this layer is c
obliquely. The condition, however, is here nearly the same as th
which I am about to describe for a more anterior section.

Figure 3 represents a section of this embryo 0.91 mm. from the p
terior end. On the ventral side of the embryo the mesoderm consists
two layers, each of which is only a single cell in thickness. These t
layers, which represent somatopleure and splanchnopleure, are separat
by a narrow space, the cœlom (*cœl.*). In the lower left-hand cor
of the figure, the beginning of this two-layered condition of the me
derm can be seen. On following the mesoderm towards the dorsum
becomes gradually thicker. In the mesoderm of this region there
found an extensive cavity (*cœl.*), which is usually irregular in outli
and might be mistaken for a *wholly* artificial condition. That the t
layers were once in contact is shown by the correspondence of outline
the two sides of the space. The separation along this line is so regul
however, in successive sections, and recurs so frequently in other e
bryos, that the cavity must be regarded as an artificial expansion of
already existing split, rather than as an indifferent rupture of a so
mass of cells. In many sections of this embryo it is easy to trace a li
of division reaching from the ventral cavity (cœlom) to the large late
cavity just described. This, then, represents a portion of the cœlo
(normally, I believe, closed), and the layers of mesoderm on the t
sides of it are consequently somatopleure and splanchnopleure. T
mesoderm in this region, as I have stated, is several cells deep. Alo
the inner and outer edges of the wedge-shaped plate of tissue constit
ing the mesoderm of either side, the cells, except where artificial ru
tures occur, are in close contact, and form an epithelial lamella. T
central portion of the plate, where this is more than two cells in thic
ness, contains cells of a more rounded shape, which do not form defin
rows, but which are closely applied to the outer layer, — a conditi
which becomes quite evident when the cœlom is artificially enlarg

The somatopleure of this region, then, is a layer at least two cells in thickness. The splanchnopleure, on the other hand, in this as in later stages, consists of a layer one cell in depth, extending from the ventral surface of the animal to the protovertebral plate.[1] Naturally no sharp line of division can be drawn at this stage between the protovertebral plates and the adjacent portions of the lateral plates. In the section under consideration, the protovertebral plate is rather compact, and it is difficult to indicate with certainty the boundary between the somatic and splanchnic layers. A study of this portion of the mesoderm, however, has convinced me that the cœlom (*cœl.'*) is already outlined, and lies in such a position as to leave only a single layer of cells dorsal to it, — a condition which is perfectly evident in later stages. It is indicated by such a distribution of pigment as is seen to the right in Figure 3.

On following the series of sections farther towards the head, a constriction of the mesoderm appears beneath the lateral margin of the medullary plate, and the open cœlom is continued into the protovertebral plate. In a section 1.2 mm. from the posterior end the somatic and splanchnic layers are each but one cell thick in the region of the protovertebral plate. The cells of the somatic layer, which in the protovertebral portion are of a high columnar form, become tile-like beneath the pronounced lateral thickening (compare Fig. 1, *cras. gn.*) of the medullary plate. The somatopleure immediately lateral to the medullary plate is rather thick, and becomes thinner both towards the median dorsal and median ventral lines. The regularity of the bounding walls of the body cavity in this region, and the occurrence of a space where no other signs of distortion are apparent, lead me to believe that the separation of the two layers of mesoderm is here perfectly normal, and not, as in more posterior regions, an artificial separation of two closely applied lamellæ.

It is, in general, very difficult to observe karyokinetic conditions in mesodermal or yolk cells, owing to the presence of the large and numerous yolk spherules; but I am reasonably certain that I have observed cells in the somatopleural thickening, dividing in a plane parallel to the surface of the layer; i. e. the cells were dividing in such wise as to increase the thickness of the layer.

In a section 1.32 mm. in front of the posterior end, the lateral portion of the medullary plate is greatly thickened, and the lateral plates a thereby wholly cut off from the protovertebral plate. The thickening of tl medullary plate is the hinder portion of a considerable ganglionic mas which is the basis for the subsequently differentiated ganglia Gasser acusticum, and nodosum.[1] The somatopleural thickening may be trace to a point about 80 μ farther forward, where the body cavity is no longe expanded. The relations of this thickening to the nephridial organs wi be discussed in connection with Stage II. (page 211).

---

[1] The differentiation of the protovertebræ has not yet begun in this region, and I shall designate the thick masses of mesoderm on each side of the chorda as protovertebral plates.

In a slightly older embryo, measuring 2.34 mm. in length, the cond tion of the mesoderm is nearly the same as in the one last describe The somatic layer shows a marked thickening (Plate I. Fig. 1, *cras. so'plu.* which is greatest immediately lateral to the protovertebral plate. A anterior cœlomic chamber is also present. The anterior limit of tl thickening is situated, as before, about 0.1 mm. in front of the hind end of the enlargement which is destined to give rise to the crania ganglia. The thickening (Fig. 1, *cras. so'plu.*) of the somatopleure slightly more pronounced than in the younger embryo.

The results of this study may be summarized as follows. Ther exists already at this stage a slight somatopleural thickening, which maximum along a line immediately lateral to the protovertebral plat This thickening is associated with a local expansion of the cœlom. I is most pronounced in the region directly posterior to the cranial ganglionic mass. Posteriorly it is lost in a general lateral thickening of th somatic layer. The location of the thickening corresponds closely wit the region in which the pronephros and segmental duct later aris Whether we have in this thickening the first rudiment of the excretory system will be discussed in connection with Stage II.

---

[1] I may here note that I have been able to make out for the series of spinal an cranial ganglia in Rana, Bufo, and Amblystoma an origin not unlike that describe by Beard ('88, pp 166, 183) in Selachii and Aves, and by Schultze ('88, p. 349) i Rana. The ganglia are developed from the ectoderm at the lateral margins c the medullay plate (Fig. 3, *fnd. gn. spi.*). The differentiation of the ganglia already apparent before the neural tube is infolded A spinal ganglion does nc arise as an outgrowth from the neural tube, nor as a separate thickening of indiffe ent ectoderm, but is differentiated from a first rudiment (Anlage) common to it an to the neural tube.

Stage II.

Plate I. Figs. 4, 5. Plate II. Figs. 13, 14.

This stage includes embryos with a distinct medullary groove, the edges of which, however, have not yet fused to form a complete neural tube. Several protovertebræ can be distinguished.

In treating of the structure of the pronephros in this stage I shall first consider two embryos, which, judging from external appearances, seem to have reached the same stage of development. These embryos are about as far advanced as the one figured by Hertwig ('83, Taf. V. Fig. 6). In both the medullary groove is widely open. They are about 2.5 mm. long, and have been sectioned, one transversely, the other frontally.

Following the series of cross sections forward from the tail end, and comparing them with those of the preceding stage, the changes which have occurred will be apparent. In the posterior region, the mesoderm, as it passes outward and downward from the chorda, tapers much more rapidly than in the earlier stage. Even as far posteriorly as a few sections in front of the blastopore, this condition can be observed; and, in a section 0.72 mm. from the posterior end, the thick central mass of mesoderm, the protovertebral region (Fig. 4, *la. pr'vr.*), has a triangular outline in cross section, and is readily distinguishable from the lateral plate (*la. l.*), with which it is continuous at its outer angle. The protovertebral plate consists of an outer epithelial layer and a central mass of cells. It is the former which is prolonged into the lateral plates. Each of these is here in general only one cell deep. Between somatopleure and splanchnopleure a few scattered cells occur, which can be assigned only with difficulty to either layer.

At 0.96 mm. from the posterior end the hindermost protovertebra visible in cross section can be distinguished. Between this point and the ganglion nodosum four protovertebræ are to be observed. Passing farther forward, it is difficult to assign boundaries to the protovertebræ. There is certainly one which is partially broken up into mesenchymatic tissue.[1] Still farther forward the series of the protovertebræ is continued by mesenchyme of a yet looser structure. Inasmuch as I have reached no conclusions respecting the number and position of the hea somites, and since great diversity of opinion exists in the accounts t be found in the literature, I shall make no attempt to number th protovertebræ with which I shall have to do in any other way tha by beginning with the most anterior that is readily distinguishabl Disregarding, then, the one which is wholly broken up into mesenchymatic tisue, somite I. lies in the same transverse plane as the fu dament[1] of the ganglion nodosum, and extends backward to the hind end of that structure. This protovertebra also shows signs of extensiv conversion into mesenchyme, although part of it at a later stage undergo muscular differentiation. Somite II. is the first of the series of we developed trunk protovertebræ. In the specimen under consideratio somites I. to VI. are already differentiated.

---

[1] I use this expression merely as descriptive of tissue of a certain histological character, quite independently of its origin. Indeed I am convinced, from observations which appear in the sequel, that not merely the head mesenchyme, but also much of that in the trunk, arises in relatively late stages from mesodermal tissue, substantially in accordance with the account of Balfour ('78, pp. 107 *et seq.*), which has recently found champions in Ziegler ('88) and others.

As I have stated, the somatopleure in the middle of the trunk consis of a layer one cell deep, to which a few loose cells lying between it an the splanchnopleure may possibly also be assigned. In the region (somite IV. the somatopleure becomes thickened. The thickening greatest at the level of the lower margins of the protovertebræ (compare Plate II. Figs. 15, 16), and tapers both dorsally and ventrally It is to be remarked in this connection that the protovertebræ are no yet fully separated from the lateral plates; but that in cross section through the middle of a somite, — i. e. midway between the anterior an posterior faces of a protovertebra, — the cœlom can be traced to th dorsal margin of the protovertebra, and furthermore that the somatopleure and splanchnopleure are seen to be continuous with the somati and splanchnic layers of the protovertebræ. The somatopleural proli eration extends forward as far as the anterior face of somite II. Th cells in the thickening have a columnar shape, and are at least two dee In some sections I have observed, in addition, a third row of thi cells next the body cavity. Near the ventral limit of the thickenin a nearly horizontal line of division in the substance of the thickenin can be observed. When seen in cross section, this line is slightly concave above. It is here that ruptures produced by artificial causes ar likely to occur, and the line thus indicated marks, I believe, the lowe limit of the pronephros. The somatopleural thickening is the fundament of the pronephros, and I shall call it in the following pages th

---

[1] In the following pages I shall use the word *fundament* as an equivalent of th German expression *Anlage*, the term *fundamentum* having been adopted as th basis for the lettering of the figures of such structures in the "Contributions from this Laboratory.

pronephric thickening. The dorsal portion of the expanded body cavity is the pronephric chamber.

The question whether the somatopleural thickening described in Stage I. be an early condition of the pronephric thickening is only to be answered by considering the fate of the former. Behind somite IV. this early thickening wholly disappears, and the one which is seen at a later stage is an independent formation. This conclusion is justified by a comparison of Figure 4 (Plate I.), showing the somatic layer to be only one cell thick in the posterior region of an embryo of the present stage, with Figure 3, which shows a two to three layered somatopleure (*so'plu.*) in a somewhat more anterior region of an embryo of the next younger stage. In the region of somites II., III., and IV., however, the somatopleure never wholly thins out; but the thickening is here moulded into a more definite form, and becomes the fundament of the pronephros. To my mind, it is as if the mesoderm, in the process of becoming thinner, was overtaken by the necessity of affording material for the formation of the pronephros and duct, and, as a matter of physiological economy, used for that purpose an accumulation of cells already present. Indeed, from the form of the thickening in anterior portions of the embryo, I am disposed to regard the differentiation of the pronephric thickening in this sense as having begun already in Stage I.

The corresponding series of frontal sections shows five well developed protovertebræ, representing somites I.–V. (Plate II. Figs. 13, 14). A mass of mesenchymatic tissue in front of somite I. is doubtless the remnant of the rudimentary anterior protovertebra observed in the series of cross sections, and behind somite V. the differentiation of a sixth is faintly indicated. Above the level of the lower border of the chorda the protovertebræ are sharply marked off from one another, and the somatic layer is relatively thin. Near their ventral margins, however, the successive protovertebræ are in close contact, and the somatic layer shows a pronounced lateral thickening (Fig. 13, *cras. pr'nph.*).

On passing ventrally to the region of the lateral plates, the inter-protovertebral constrictions vanish. Since frontal sections, however, do not here cut the layer of mesoderm perpendicularly, certain sections in the series show a distinctly segmented splanchnic layer, while the somatic thickening in the same frontal plane is unsegmented. Farther ventral there are no traces of segmentation in either layer. Here the splanchnopleure (*spl'plu.*) uniformly consists of a single layer throughout its entire extent. The somatopleure facing the ganglion nodosum, and also that in the posterior region, is thin; but in the anterior portion of the trunk, immediately behind the ganglion nodosum, there is a marked thickening (*cras. pr'nph.*), which ends abruptly in front, but gradually thins out into indifferent somatopleure behind. This thickening is distinctly present through a length of 0.5 mm., which is slightly greater than the extent of protovertebræ II., III., and IV. Still farther ventrally, the antero-posterior extent of the thickening is much diminished, the reduction taking place from both ends, so that in passing ventrally the region in which the structure is last visible is situated approximately beneath protovertebra III.

Another pair of embryos, one of which was 2.5, the other 2.6 mm. in length, presented a condition of the pronephros somewhat more advanced than that just described (Plate I. Fig. 5). In these embryos the lips of the medullary fold in the most advanced region were in contact, but had not yet fused. The anterior limit of the pronephric thickening was the same in position as in the younger pair of embryos, lying near the middle of somite II. A study of the arrangement of the nuclei in this region made it evident that there were at this stage in general three layers in the thickening. The innermost of these is the thinnest, and is destined to become the peritoneal covering of the pronephros; the other two represent the two walls of the pronephric pouch, soon to be described. The pronephric thickening in the region of the anterior face of somite IV. is shown in Figure 5. The section gives a somewhat false impression as to the somatic layer of the protovertebra, unless the relation of the section to the successive somites be borne in mind. The considerable thickening which this layer apparently undergoes on passing into the protovertebra is due to the circumstance that the section here passes obliquely through a portion of the anterior wall of somite IV. Sections through the middle of a protovertebra show a gradual thinning of the somatic layer as far as the dorsal angle of the mesoderm (compare Plate II. Fig. 15, which is a cross section of the following stage), where this layer is almost pavement-like. The pronephric thickening extends rather farther posteriorly than in the former pair of embryos, and while it is manifestly difficult to set a limit to the structure, I am confident that the thickening extends into somite V. This posterior extension of the thickening is to be regarded as the fundament of the *pronephric*, or, according to the later nomenclature of Balfour, the *segmental duct*.

The corresponding series of frontal sections shows six well differentiated protovertebræ, representing somites I.–VI. The same group of cells which I interpreted before as the last remnant of a rudimentary anterior somite is still present, and a few more posterior protovertebræ are in process of formation. Frontal sections just ventral to the chorda are very instructive. By following through a series of these, an idea can be had of the successive changes which take place in passing from the protovertebræ to the lateral plates, — a region of prime importance for problems respecting the development of the urogenital organs. In sections approximately tangent to the chorda at its ventral border (compare Fig. 5), the plane of the section passes through the ventral floor of the protovertebra, and cuts the somatic mesoderm near the place where the protovertebra passes into the lateral plate. The body cavity is expanded in the anterior part of the trunk. The mass of tissue on the median side of the body cavity appears very broad, owing to the circumstance that the plane of the section, as before noted, lies in the floor of the protovertebra. The somatic layer is several cells thick, and very compact in structure, owing to the fact that the section passes through the dorsal margin of the pronephric thickening. In following the series of sections farther ventrally, the boundaries between the segmental constituents of the pronephric thickening become indistinct; and in a section 90 μ farther ventral they have wholly vanished. This section, however, still shows traces of segmentation in the splanchnic layer, which is here reduced in thickness, the plane of this section having passed ventral to the floor of the protovertebra. Still farther ventrally the segmentation of the splanchnôpleure likewise vanishes, and finally the pronephric thickening gives place to undifferentiated somatopleure. I have looked in vain for prolongations of the body cavity into the pronephric mass at this stage. I believe that the pronephric thickening is to be regarded as a solid proliferation of the somatopleure, in which, however, the somatic layer of the protovertebræ takes some part.

Stage III.

Plate I. Fig. 6. Plate II. Figs. 11, 12, 15-17.

In embryos of this stage the medullary canal is wholly closed, the fundaments of two pairs of gills are present, and the auditory vesicle consists of a shallow depression of the deep ectoderm.

The pronephric thickening has now begun to assume a more definite form, and during this stage becomes converted into a tubular organ. I shall first consider the structure as seen in a series of cross sections from an embryo measuring about 2.7 mm. in length. Figures 15 to 17 are from this series. The anterior end of the pronephric thickening is located in somite II. The plane of the section from which Figure 15 was drawn passes somewhat behind the middle of this somite, so as to show the location of the constriction between the protovertebræ and the lateral plates. In the middle of the somite, the arrangement of the cells composing the pronephric thickening appears to be that of a fold in which the layers are in close contact. The thickening is composed of three layers of cells, and it is possible to trace the somatic layer of the protovertebræ into the outer layer of the thickening. The lateral indifferent somatopleure is continuous at the ventral border of the thickening with the inner or thin layer which lies next to the body cavity. Near the upper border of the thickening this inner layer appears to be folded abruptly on itself to form the middle layer of the thickening. The middle and outer layers are continuous with each other distally, i. e. ventrally.[1] This anterior knob of the pronephric thickening (Fig. 15, *fnd. nph'st.*[1]) is the fundament of the first nephrostome, a later stage in the development of which is shown in Plate III. Fig. 18 (*nph'stm.*[1]). In Figure 15 the three layers are indicated by the arrangement of the nuclei. Of these the two outer form the fundament of the first nephrostomal tubule. The innermost layer represents the underlying peritoneum. In the region between somites II. and III., it is impossible to distinguish definite layers in the thickening.

On entering somite III., the pronephric thickening has a far greater breadth, and it consists of three layers, the meaning of which is to be understood by a comparison with the condition in the region of the first nephrostome, just described.

In somite IV. (Fig. 16) a division of the thickening into a dorsal and ventral part is indicated, near the termination of the dotted line (*cras pr'nph.*). The dorsal part is the fundament of the third nephrostome and the ventral part represents the anterior portion of the segmental duct (more properly, common trunk, see page 228). The ventral portion of the thickening can be traced backwards from this point through a distance of about 0.37 mm. Figure 17 is drawn from a section through a region near the anterior boundary of somite VII., and shows

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[1] The correlative terms *distal* and *proximal* are so frequently employed by German writers as synonymous respectively with *posterior* and *anterior* that it seems advisable to allude to the fact that they are not used in the present paper in that sense, but invariably with their primitive signification; thus, the distal portion of a process is that part which is most remote from the point of attachment, whether the structure project anteriorly or posteriorly, medially or laterally, dorsally or ventrally.

the thickening (*cras. pr'nph.*) near its posterior termination. The mass is evidently a thickening *in situ* of the somatopleure. On either side of the fundament of the segmental duct the somatopleure is one cell thick, whereas in the fundament itself it is two or three cells in thickness. If the additional cells arose by a free backward growth from the anterior pronephric mass, we should expect to find them lying on the external face of a continuous somatopleural layer. But, as a matter of fact, no such continuous inner layer exists; on reaching the thickened region, the somatopleure merely becomes several cells in thickness, the outer cells presenting really a somewhat more compact condition and a more linear arrangement than the inner ones.

The constrictions between the protovertebræ and the lateral mesoderm can be distinctly made out only in intersegmental regions. As is shown in Figure 15, between somites II. and III. the level of the constriction is immediately dorsal to the nephrostomal portion of the pronephric mass. In the region between somites III. and IV. the division occurs at a corresponding position. This series of sections shows no sharp separation between protovertebral and lateral mesoderm posterior to somite IV., the protovertebral plate being here only partly broken up into successive metameric blocks, which do not as yet possess sharp ventral boundaries.

In frontal sections, the pronephric thickening shows a similar condition (compare Figs. 11–14) to that which obtains in the case of the embryo described under Stage II. (page 213), the most noticeable difference being an increase in the thickness of the pronephric mass. The longitudinal extent of the thickening corresponds approximately to that of five somites, though the posterior limit is of necessity somewhat uncertain. The posterior portion has every appearance of having arisen in the same way as the part lying beneath somites II., III., and IV. The latter, however, represents, as we have seen, the future pronephros; the former is the fundament of the segmental duct.

In an embryo slightly older than those last described, the evidences of an incipient canalization of the pronephric system are more pronounced. In the region of somites II.–IV., the two outer layers of the pronephric thickening are separated from the peritoneal layer by a distinct line of division. In the intersegmental regions, the outline of these two layers is that of an elongated ellipse, the nuclei being disposed, for the most part alternately, on either side of its major axis. The significance of this distribution becomes apparent on studying later stages, in which a lumen has appeared in the organ. It is then found that the lumen occup the position of the major axis of the ellipse, and that the nuclei of t bounding cells lie close to the interior surface of the wall. If a tube constituted be compressed laterally, so that the lumen wholly dis pears, it is evident that the cells of the opposed walls would be likely accommodate themselves to one another so as to present an altern arrangement of their nuclei.

Opposite the middle of a somite, the relations are somewhat differe Here the two layers of what I shall hereafter call the pronephric pou do not remain confluent at its dorsal extremity, but separate, the ou becoming continuous with the somatic layer of the protovertebra, t inner with the deepest layer of the thickening, and thus finally with t lateral somatopleure. In this region the body cavity can be seen project for a short distance between the two layers of the proneph pouch, as shown in Plate I. Fig. 6, *cœl.* This figure demonstrates ve clearly the relations of the pouch to the lateral mesoderm and the ov lying somites.

In the case of the younger set of embryos which have been c sidered in this stage, it will be remembered that the boundary betwe the lateral mesoderm and the protovertebræ was evident only in int segmental regions. In the somewhat older individual now under c sideration, the constrictions between these two portions of mesoderm ha advanced into segmental regions as well; so that now, for the first tin the precise relations between the fundaments of the nephrostomes a the protovertebræ lying above them can be accurately determined. T last remnant of the communication between the protovertebral cav and the body cavity I shall call the communicating canal, following this the nomenclature of Renson ('83). The section shown in Figure passes through this canal (*can. comn.*), and it is to be especially not that the constriction between the somites and the lateral plates tak place dorsal to the region of communication between the pronephric s tem and the body cavity. Immediately dorsal to the pronephros, t somite sends out a lateral fold of the somatic layer, which is destined form the capsule of the pronephros, to which I shall have occasion refer in later stages.

In somite IV., the division of the pronephric mass into a dorsal a ventral part is faintly indicated, but the dorsal part shows no trace the lumen which is destined to become the third nephrostome. In t embryo, the constrictions between the protovertebræ and lateral pl have advanced into more posterior regions. In somite V. the constr ion occurs immediately dorsal to the fundament of the segmental duct, hich, as I have shown, is continuous anteriorly with the ventral half f the thickening appearing in somite IV. A series of measurements rom the dorsal median line shows that the ventral portion of the pro- ephric thickening remains at a nearly constant level, so that the pro- overtebræ must reach a somewhat more ventral position in the posterior egion than in somites II.–IV.

Figure 11 (Plate II.) represents a frontal section through the dorsal art of the pronephric pouch in one of the oldest embryos of this stage. t shows the course of the earliest fundaments of the three tubules which merge from the somatopleure beneath protovertebræ II., III., and IV. he most anterior outgrowth, arising in somite II., inclines outward and ackward into the region of somite III.; the second outgrowth proceeds rom its origin beneath protovertebra III. directly outward; and the hird outgrowth inclines forward, so that its distal extremity also lies in he region of somite III. As the review of the previous stages has hown, these fundaments of the tubules have *not arisen as separate out- rowths* from the somatopleure, but have been differentiated from the riginally continuous pronephric thickening, the three fundaments being onfluent distally.

In this section the nuclei are abundant along a central band, but scarce r wholly absent in peripheral parts. This peculiar arrangement be- omes intelligible when we consider that the plane of the section passes lmost tangentially through the curved dorsal wall of the pouch. As we ave seen in transverse sections, the nuclei lie close to the inner lumen f the pouch; it is therefore only in the deeper central parts of the sec- ion that they are encountered. In a section 0.03 mm. farther ventral Fig. 12), the lumen of the pouch can be made out, though it is not con- picuous. It is difficult to say whether at this stage the lumen is contin- ous throughout the whole structure. In many embryos the evidence of uch continuity seems indubitable; whereas in others, apparently quite s far advanced in other respects, the lumen seems to consist of uncon- ected portions. In some instances where no trace of a separation of the walls could be seen, a line of pigment indicated the position of the lumen. Occasionally I have met with a distinct prolongation of the body cavity into the pronephric mass. This condition has been most frequently encountered in the case of the fundament of the first tubule. I am not, however, inclined to place much weight on such observations as proving the claim that the lumen of the pronephros forms as an ingrowth of the cœlom proceeding from the nephrostomes and advancing into the duct.

On the contrary, the lumen is already potentially present, as show the arrangement of the nuclei before any actual separation of the occurs. I am of opinion that, in the cases referred to, the separati largely artificial, and that the ruptures take place most frequently a nephrostomes for the reason that the walls, which elsewhere form a c ring, here have in cross section the form of a sharp re-entrant angle dering on a large open space. It is evident that in the former regio walls would be less liable to be torn apart in the preparation of the terial than in the latter. In general, however, it must be admitted the development of the lumen, like that of the system as a w actually advances from anterior to posterior regions.

The fundaments of the three pronephric tubules shown in Figu are not to be regarded as outgrowths from the somites. They are, true, very closely related to the segments in their arrangement, b transverse sections prove (Plate I. Fig. 6, and Plate II. Fig. 15), lie wholly ventral to the lower boundaries of the protovertebræ. frontal section figured (Fig. 12) was chosen for the reason that i the one which indicated most precisely the course of the fundame the three tubules. The plane of the section is parallel to a ta to the dorsal margin of the structure, and passes only a little below margin, not through the nephrostomes. These begin in a more ve unsegmented region.

In the oldest embryos of this stage, the fundament of the duc developed very rapidly. Anteriorly, it has in cross section a disti elliptical outline, and its cells have, with reference to the major a the ellipse, the same arrangement that I have described for the i segmental regions of the pronephric pouch. On following the stru backwards, this distribution becomes less and less obvious, unti cells seem to have no definite arrangement. In this region the f ment of the duct is in far more intimate union with the somatop than was the case in anterior somites. In the region of somite the last trace of the structure is to be seen as a simple thickeni the somatopleure, similar in form to that described and figured i youngest embryos of this stage (Fig. 17), for a region just ba somite VI. The region in which the duct is formed is throughou mediately ventral to the constriction separating the protovertebræ the lateral plates.[1]

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[1] In sections from the posterior end of the embryo, it is necessary to against the false appearances which arise from the obliquity of the plane

The mode of development which I have described in the foregoing pages, taken in connection with frontal sections, which show that the pronephric thickening tapers gradually backwards into indifferent somatopleure, seems to me to be very strong evidence concerning the precise origin of the duct. I believe I am justified in concluding that *the segmental duct between somites V. and IX. arises in situ from a thickening of the somatopleure serially equivalent to that from which in the anterior region the pronephros is developed.* Indirect evidence which can be brought to bear on this question will be reserved for the fuller consideration which can be accorded it, in connection with the following stage (page 222).

STAGE IV.

Plate I. Figs. 8, 9. Plate III. Figs. 18-26. Plate IV. Figs. 29, 39.
Plate V. Fig. 45.

I have placed in this stage embryos of frogs taken from five different killings. They all belong to the fourth day after fertilization, and aside from individual variation show an evident advance in organization on the preceding stage. In all a distinct differentiation of muscular tissue has begun, the auditory vesicle is wholly cut off from the epidermis, and the ventral sucking (or more properly sticking) disks are well developed. In the following description, I shall find it convenient to distinguish a younger and an older set of embryos. In the younger set the embryos are from 3¼ to 3½ mm. long; they have about 14 protovertebræ and the fundaments of 3 pairs of gills. The embryos of the older set are from 3½ to 3¾ mm. long; they possess about 17 protovertebræ and the fundaments of 4 pairs of gills.

All the embryos of this stage have the pronephric pouch in its typical form. A side view of this organ with the neighboring portion of the

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section to the vertical axis of the protovertebra. Cross sections in this region frequently encounter two contiguous protovertebræ. If the plane of the section traverse the communicating canal of a protovertebra, it would also pass obliquely through the dorsal portion of the next anterior protovertebra. The latter would then appear in cross section as a distinct mass immediately lateral to the neural tube and the chorda, and would resemble the condition which a protovertebra presents when cut near its anterior or posterior wall. Immediately below this mass there would be found on the same cross section the ventral portion of the more posterior protovertebra, with the corresponding part of its cavity. The latter, however, being apparently a direct continuation of the body cavity, owing to the existence of the communicating canal, would appear to represent the dorsal part of the body cavity, and the fundament of the duct would thus seem to be farther removed from the dorsal angle of the body cavity than it really is.

segmental duct is shown in Figure 39 (Plate IV.). In this drawi
the outlines were obtained by reconstruction from a series of cr
sections. The pronephric pouch is suspended from the dorsal an
of the body cavity by the nephrostomal funnels. Elsewhere it is who
cut off from the mesoderm, and merely rests conformably on the ou
surface of the somatopleure. The precise relations of the parts can
understood by referring to the series of cross sections shown in Figu
18 to 22 (Plate III.). Figure 18 represents a section through the
pronephros in the region of the first nephrostome. The location of
plane of this section in the reconstruction is indicated by the dot
line *18*, in Figure 39. The lateral plates are here wholly cut off fr
the protovertebræ, splanchnopleure and somatopleure being continu
with each other at the dorsal angle of the body cavity. Figure
shows the structure of the organ between the first and second neph
stomes. In this and the following sections it was found advisable
depict the pronephric structures of the *right* side in order to exh
in each case the section which most clearly showed the structural c
ditions. The next drawing (Fig. 20) in the series represents a sect
through the second nephrostome. In the preceding section, — not
ured, — the three portions into which the lumen is here divided
continuous. The constriction between the middle and the ventral lun
is artificial; for the cells occasioning this local closure do not belong
the proper wall of the pouch, but form a group within the cavity.
several instances I have observed such groups of cells lying entirely f
in the lumen of the pouch (Plate V. Fig. 45). In the present ca
however, the mass is very intimately connected with the adjoining wa
This condition is preserved through a distance corresponding to t
thickness of two or three sections, but the mass terminates by becomi
free from both walls, so that in cross section it has the appearance of
"island" of tissue occupying the lumen of the pocket. The occurren
of these islands within the cavity of the pouch is of significance
determining precisely how the organ is developed. It is difficult to co
prehend how they could be formed, provided the canals were produc
by a fold of the somatopleure. On the other hand, they are perfect
intelligible on the assumption that the canals arise by the rearrang
ment of a solid mass of cells into a peripheral layer with a centr
lumen. According to the latter view, the islands would represe
residual portions of the pronephric thickening which had not been tran
formed into peripheral wall.

Returning now to the section last under consideration (Fig. 20), t ventral union of the walls of the pronephric cavity is, as I have shown, artificial; the constriction between the middle portion of the lumen and the dorsal, or nephrostomal, portion is more apparent than real, for it is formed by the posterior wall of the nephrostomal tube, the plane of the section not having cut exactly in the axis of the tubule. In the section following that shown in Figure 20, the pouch is detached from the peritoneum, and presents an appearance similar to that shown in Figure 19. Before the third nephrostome is reached, the canal is divided by a horizontal constriction into two tubes. The dorsal portion forms the tubule of the third nephrostome; the ventral portion is the anterior end of the segmental duct. Figure 21 shows these parts in the region of the third nephrostome. The section corresponds in position with the dotted line *21* in Figure 39.

In the following sections the duct rapidly assumes a more dorsal position (compare Fig. 39). It then proceeds directly backward, at the level of the constriction between protovertebræ and lateral plate. Figure 22 shows the duct in the region of somite VI. It has not yet been formed, however, throughout its entire length. On passing posteriorly, it gradually loses its lumen; then the circular arrangement of the nuclei indicating the position of the lumen also vanishes; the structure at length terminates as a simple thickening of somatopleure in the region of the tenth somite. In a few individuals, however, I found slight evidences of a mode of ending different from that just described. In one case the indications seemed so strong as to compel me to seek confirmation of the view that the duct takes its origin *in situ*. I shall therefore give the details of the evidence on this point, and discuss its probable significance.

Figure 23 represents in cross section the fundament of the duct in this specimen, as shown in the fifth section in front of its termination. The section of the mass here contains about eight cells, which are in close contact with the somatopleure. In the second section behind this one there are shown parts of four or five cells (Fig. 24). The protoplasmic patch in the centre *(cd.)* is wider than an average cell of the fundament, and probably represents the anterior ends of two cells lying in the following section (Fig. 25, *c.* and *d.*). Dorsal to this mass of protoplasm is a nucleated cell (*b.*), and above this a small area of protoplasm with a faint nucleus (*a.*) which is doubtless a portion of a cell the principal part of which was cut off by the preceding section. On the ventral side of the centre of the fundament there is also a round nucleated cell (*e.*). In the next following section (Fig. 25), there are two nucleated cells in the centre of the mass (*c.* and *d.*), which, as I have said, doubtless corr spond to the central protoplasmic area (*cd.*) seen in the preceding se tion. The most prominent cells of that section are here represented b two faint circles of protoplasm (*b.* and *e.*). In the next following sectio not figured, the duct terminates as a single non-nucleated mass, probabl corresponding to the dorsal cell in Figure 25. This remnant lies in distinct depression of the somatopleure (Fig. 26, *f.*). This depressio continues backwards through the space of three sections. Instead, the of terminating in a thickening of the somatopleure, the end of the du lies in a groove of unmodified somatopleure. There is no tissue directl behind the duct for its further growth, and the inference is natural th the somatopleure is mechanically depressed before the growing tip of t duct. In fact, I believe this to be actually the case, and that in th region the duct does grow by a simple cell proliferation within its ow mass.

The key to the situation is to be found in the location of the po terior end of the duct in this specimen. An enumeration of the somite shows that the sections figured lie at the hinder end of somite XI. T show the bearing of this fact, I shall anticipate some of the result of a study of Stage V. In a series of frontal sections of the latte stage, I have succeeded in locating with reference to the successiv somites the position at which the duct opens into the cloaca. The ope ings are in the same vertical plane with the middle of somite XII. Th posterior end of the duct, then, in the specimen which I have just de scribed, is within the distance of half a somite from its final terminatio In order to empty into the cloaca, the duct has to grow inward from it position at the lateral margins of the protovertebræ to a position muc nearer the median plane. It is difficult to comprehend how the duc could make this extension, except by proliferation of its own cells. It i just in this region that I find evidences of such a mode of growth. If th inference I have drawn from the facts adduced be correct, it seems t me to add strength to the conclusion I have reached in regard to th general mode of formation of the duct, inasmuch as it has been shown t be possible to detect free growth where it exists.

That the duct arises in the way I have described, and is not develope from the ectoderm, is shown, moreover, by certain indirect evidence whic may be properly discussed at this point. As I have already stated, th duct is developed in such intimate connection with the somatopleur that I have been led to believe that it arises throughout its entire lengt from a proliferation *in situ* of that layer. In almost all of my prepa rations the duct in its backward growth is separated by a considerable space from the ectoderm, and I have observed no instance in which it was impossible to distinguish a perfectly sharp line between the fundament of the duct and the overlying ectoderm.

In describing the germ layers in Stage I., I referred to certain histological criteria which might be employed in determining to which germ layer a given group of cells belonged. The most valuable of these is the difference in the size and abundance of the yolk spherules, which even in that early stage served to contrast sharply the mesoderm from the ectoderm. In later stages, this character is equally pronounced. When the duct appears, the cells which constitute it are not distinguishable in histological features from those of the adjacent mesoderm, but are very different from those of the neighboring ectoderm. It seems to me extremely improbable that the cells of the fundament of the duct, with their numerous large yolk spherules, should have been recently derived from those of the ectoderm, which are provided with only few spherules of much smaller size. It would be entirely contrary to our conceptions of the physiological nature of yolk, if in the course of embryonic development this material was increased instead of diminished in quantity.

A similar argument seems to me to afford evidence that the duct arises *in situ.* If the duct had grown freely backward from an anterior proliferation, such growth would in all probability have been associated with the consumption of yolk in the cells of the fundament, and the spherules would be smaller or less numerous than those of the adjacent mesodermal cells. This, however, is not the case.

I conclude, therefore, that the segmental duct arises throughout its entire length by a proliferation *in situ* of the somatopleure. Its posterior end, however, grows across to the cloaca free from adjacent tissue.

Returning to the pronephric pouch, I purpose describing the relations of that organ to the somites. The section represented in Figure 29 (Plate IV.) shows graphically these relations. The plane of section in this case was very nearly tangential to the somatopleure at the points where the nephrostomes emerge. In this section it is evident that the three nephrostomes lie precisely under the first, second, and third somites, behind the ganglion nodosum. These correspond to the somites which I have numbered II., III., and IV.; so that the pronephric pouch remains in the same position as the pronephric thickening of earlier stages. In Figure 21 (Plate III.) the last remnant of the canal connecting the body cavity with the cavity of the protovertebræ is faintly indicated (above the letters *cœl.''*) in the same transverse

plane as the third nephrostome; and Figure 6, as we have seen, sho
more plainly the same condition in the case of the second nephr
stome at an earlier stage.

The structure of the protovertebræ in this stage (Plate V. Fig. 4
merits especial consideration. Already in younger stages there is
differentiation of a peripheral epithelial layer surrounding the dense ce
tral mass, or kernel of the protovertebra. Laterally this peripheral pa
is represented by the entire somatic layer, which is separated from t
kernel by the protovertebral cavity (*cœl.*). Along the median and ve
tral boundaries of the somite, a layer having an epithelial character
also to be seen. Thus the central mass which is to develop into the my
tome lies on the median side of the cœlom, and is wholly surrounded
an epithelial layer. Frontal sections show that this layer can be trac
inward for some distance between successive somites, both from th
median and lateral surfaces. Since the development of the protoverteb
proceeds from before backwards, a single frontal section shows successi
stages in the changes which they undergo. From such a section it
apparent that neither the median nor the lateral portion of the p
ripheral layer develops muscular fibres. That portion of this lay
however, which is included between the kernels of successive pro
vertebræ, is apparently differentiated into muscle, and becomes merg
in the myotomes. Very soon after the first development of mus
fibres in the myotomes, the peripheral portions which have not be
converted into muscle separate from the central mass, and, while yet a
hering in a lamella, show evident signs of disassociation. It is to
noted, that, in regions where traces of the communicating canal are s
distinguishable, the median peripheral layer, not the kernel, is seen to
continuous with the splanchnopleure. The somatopleure, on the oth
hand, may be traced, as before, into the outer layer of the protoverteb
This peripheral layer I believe to be wholly converted, with the exce
tion stated, into mesenchymatic tissue. In the stage before us we s
that it is distinctly breaking away from the myotome, and that the ce
are acquiring a flat tile-like form. In the following stage no layer th
could properly be called epithelial is present. In its stead there is
considerable quantity of loose mesenchyme, and the lateral face of t
myotome is covered by a sheath consisting of very delicate fibrillar co
nective tissue.

Not merely is mesenchyme produced by the thin peripheral layer
the protovertebræ, but in anterior regions considerable portions of t
kernels of the protovertebræ also undergo a metamorphosis in this dir

n. Thus, if I be not mistaken, a protovertebra immediately in front somite I. has been wholly converted into mesenchymatic tissue; the rnel of the succeeding protovertebra (somite I.) has given rise to a nsiderable quantity of mesenchyme; and the process has been manited, though to a less degree, even in succeeding somites. Furtherre, having established the continuity of splanchnopleure and somatoure with the median and lateral peripheral layers respectively of the otovertebræ, it seems to me the more probable that the former as well the latter may give rise to mesenchyme. I have, in fact, seen condins directly in front of the first nephrostome which indicated a very ensive production of mesenchyme from the lateral plate in that ion.

My reason for dwelling at so great length on the derivatives of the ripheral layer of the protovertebra is, that this layer plays an imporit part in forming certain accessory portions of the pronephric system. refer to the *capsule* of the pronephros. Already in the preceding ge I noted the occurrence of a lateral fold of the somatic layer imdiately dorsal to the constriction between protovertebræ and lateral tes (Fig. 6). In the younger individuals of Stage IV. the fold covers dorsal surface of the pronephric pouch, and extends a short distance vn on its lateral surface (Figs. 18–21, *fnd. cps.*). In the older set of bryos it has reached the somatopleure ventral to the pronephros, and s forms a complete investing capsule.

n frontal sections the fundament of the capsule may be seen to sist of a series of segmental outgrowths from the successive proertebræ. Later, these segmentally arranged structures fuse into a tinuous enveloping sheet.

Lateral to the pronephros the capsule presents in general a two-layered dition, the result of its having been formed as a fold; but on ascend- to the level of the lower boundary of the somite, these two layers arate (Plate V. Fig. 45); one passes beneath the protovertebra, cover- the pronephros on its dorsal aspect; the other is continuous with the natic layer of the protovertebra, forming a lateral sheath to the myone. These layers are present in the region both of the pronephros and the duct, but are seen in their simplest condition in the region of the ond nephrostome (Fig. 20); not merely because this is the middle ot pronephros, but also because the process is somewhat modified in the otovertebra next in front of it (somite II.). Somite II. is one of those which a considerable portion of the kernel of the protovertebra is conted into mesenchyme. For this reason the inner layer of the capsular

fold, after separating from the layer which forms the lateral sheath of th
myotome, passes inward, and is there lost in a loose mass of tissue (Fi
18), resulting from the disassociation of certain cells of the somite in th
region. Intersegmental regions also present appearances which are co
fused by the occurrence of cells belonging to the partition between tw
successive somites. The points which I especially wish to emphasize
this description are (1) the origin of the capsule from the somatic lay
of segmented mesoderm, and (2) the fact that the layer from which th
capsule is developed is also in other regions converted into mesench
matic tissue.

In the younger specimens of this stage a horizontal fold of the splanc
nopleure is to be noticed, forming a slight ridge directly across the bo
cavity from the pronephros. It first appears in front of the second n
phrostome, and develops from this point backwards. It is the fundame
of the glomus or pronephric glomerulus.[1] In the earliest trace of th
organ that I have been able to find (Plate I. Fig. 8) there were alread
a few small mesenchymatic cells (*ms'chy.*) located in the angle of th
fold. The source of these cells I have been unable to determine wi
certainty. The nuclei of all the cells in the fold itself lie very close
the body cavity, and it does not seem probable that those small cel
could be produced by delamination from the splanchnopleure without
actual migration of the nuclei of the somatopleural cells to the basal,
entodermal, surface of that layer. I have never seen signs of such migr
tion, and I therefore do not believe that it occurs. Furthermore, th
folded portion of the somatopleure does not at once become thinner tha
the neighboring portions of that layer. In older stages, such a thinnin
takes place, but it seems to be due to a superficial extension of the laye
rather than to delamination. The position of the nuclei of the lar
entodermal cells in this neighborhood is equally unfavorable for th
formation of these small cells by delamination. The only remainin
explanation is that the latter have migrated into their present positio
from relatively remote parts. Other loose cells may be found betwe
entoderm and splanchnopleure, and the question here raised is only
part of the larger problem as to the source of all such cells, includin
those which bound the yolk veins. The fate of the cells which I hav
found in the fundament of the glomus, I shall consider in treating of
later stage. I may, however, here anticipate to the extent of statin
that they are connective-tissue elements.

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[1] The former term seems to me preferable, and will be employed in the follo
ing pages. The exact relations of the glomus to the mesonephric glomeruli will
explained in the general discussion.

'igure 9 shows the fundament of the glomus in one of the older em-os of this stage. Within the hollow of the fold may be seen two s (*ms'chy.*), which are to be regarded as the descendants of the first ll cells to which I referred in the younger embryo. Their differen-ion in the direction of connective tissue can be noticed throughout whole extent of the fundament. The scattered rounded cells near n probably represent embryonic blood cells in the region of the :a.

STAGE V.

Plate I. Fig. 10. Plate IV. Figs. 31-34, 40.

'he embryos belonging to this stage are on an average about thirty rs older than those of Stage IV. At this period almost all of the s are hatched; and, the duct having opened into the cloaca, the pro-hros becomes functional. The larvæ of this stage measure 5–7 mm. ength, the rapid increase in size being largely due to the growth of tail.

'he form which the pronephros presents in this stage has been studied neans of reconstructions in the case of four pronephridia. The dia-ns on Plate IV., Figures 31 to 38, represent in a rough way the num-and distribution of the convolutions which the tubules present in this the following stage. Of these, Figures 31 to 34 relate to the present ;e. Figure 40 is a more accurate view of the pronephros which I e diagrammatically represented in Figure 32. In Figure 40 the out-s were taken with but little modification from the original recon-ction. I have not hesitated, however, even in this case, to remove cts plainly due to artificial causes, such as distorted sections and curate superposition.

'omparing this drawing with Figure 39, it is easy to follow the nges that have taken place. In the earlier stage the fundaments he three tubules are already present. The first modification which be noted is the deepening of the constrictions which are indicated veen the successive nephrostomes. In this way are formed three nsverse tubules, joining distally a longitudinal canal; the former are nephrostomal tubules, the latter I shall call the *collecting trunk.* this case the continuation of the collecting trunk pursues a nearly ight course to the posterior margin of the gland, where it emerges as segmental duct.[1] A second change which is apparent in Figure 40

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[1] In Figure 40 the first nephrostomal tubule and the collecting trunk have a : color, the second tubule is yellow, and the third is orange, whereas the seg-tal duct is uncolored.

is the growth of the collecting trunk in the region between the seco and third nephrostomal tubules, and the consequent separation of t latter. The further complication in this case is mainly due to a co volution of the second tubule; slighter contortions occur in other part In the case of the pronephros diagrammatically represented in Figure 3 however, a canal, which corresponds to what we should regard in Figu 32 as the anterior portion of the segmental duct, has been folded fi forwards, reaching nearly to the level of the first nephrostome, and th backwards. The bends which are convex anteriorly may be called t anterior bends; those which are convex posteriorly, the posterior benc The universal occurrence of this condition in all older embryos mak it desirable to distinguish this bent portion of the tube and its deriv tives both from the original longitudinal canal of the pronephros, whi I have called the collecting trunk, and from the straight posterior po tion, or segmental duct proper. In the following pages I shall spe of each *nephrostomal tubule* as extending from its origin in the nephr stome to its junction with the longitudinal canal, or collecting trun In the case of the first nephrostomal tubule, the point of union with t collecting trunk is usually marked by an abrupt change of directio where this does not occur, however, the distinction between the tv portions must be somewhat arbitrary. The *collecting trunk* forms t continuation of the first nephrostomal tubule, it receives in its backwa course the second tubule, and may be regarded as terminating at t point of entrance of the third tubule. The *common trunk* arises fro the point of junction of the third tubule with the collecting trunk, an after making various convolutions, leaves the gland at its posterior en as the segmental duct. In the two pronephridia shown in Figures 31 an 33, we have before us examples respectively of the two principal forn of convolution which are to be recognized in subsequent stages, viz. t contortion of the second tubule and that of the common trunk. T third tubule finally undergoes convolution to some extent; but the fir tubule and the collecting trunk take almost no part in the proces Although complication has appeared both in the second tubule and the common trunk, it is to be noticed that these processes do not have fixed sequence. I have numbered the diagrams on Plate IV. with refe ence to the state of development shown by the larvæ. In doing this, have not been guided by the age alone, for the large amount of ind vidual variation makes that method nearly valueless; but I have e deavored, by passing in review a large number of characters, to gain notion of the relative degree of development shown by the larvæ.

The first of the series of diagrams (Fig. 31) shows complication to ve taken place to a considerable extent in both the convoluted regions. the next diagram (Fig. 32) the second tubule alone takes part in the nplication. Figures 33 and 34 represent respectively the right and t pronephridia of one individual. In the right pronephros (Fig. 33) e typical condition of the common trunk is present, while the neph- tomal tubules have undergone no contortion. Likewise in the left onephros (Fig. 34) it is the common trunk to which the increasing nplication is due; but in this case there are two additional bends roduced by a slight folding backward of the middle of the anterior nd. The convolutions of the common trunk lie principally in the ntral portion of the gland. The tubes which in cross section are seen the dorsal part are mainly the several nephrostomal tubules, and the lecting trunk. This condition is likewise retained in later stages.

The position of the pronephros with reference to the myotomes has t changed since the preceding stage. The whole structure is slightly ger, but the myotomes have also lengthened to the same extent. e three nephrostomes are situated, as before, beneath the first, second, d third myotomes posterior to the ganglion nodosum, and are seg- ntal in position.

In all the embryos of this stage the duct has opened into the cloaca. is to be remembered in this connection, that the morphological posi- n of the duct is outside the somatopleure; so that the cœlom and o layers of mesoderm intervene between it and the intestine. As ght be expected, the union does not take place until the segmented d unsegmented portions of the mesoderm have become separated m each other. The passage to the cloaca is then effected through split thus produced, and consequently around the dorsal angle of body cavity.

In the frog, there is a sharp histological contrast between ectoderm d entoderm, and there is therefore no difficulty in assigning a limit the proctodæal invagination. The region into which the duct opens he hind gut, and the intestine at this point is unquestionably lined h entodermal cells. The portion of the primitive gut posterior to the nings of the segmental duct forms the Amphibian cloaca, and corre- nds precisely, I should say, with that part of the cloaca of Amniota ich Gadow ('88, p. 28) has recently designated by the name *urodæum*. e wall of the intestine is not wholly passive in the union occurring ween it and the duct. In front of the excretory openings, the lumen the intestine has an elliptical form, its major axis being vertical.

On passing backwards, the dorsal half broadens and finally exhi two lateral processes, or cornua, the walls of which are composed layer one cell deep. The ducts open into the distal ends of these co (see Fig. 27, showing the condition in Stage VI.). Behind the ou of the segmental ducts, the lumen of the intestine has a nearly circ outline, and descends rapidly to the anus, or, as it may now more rectly be called, the cloacal aperture. I was able to see in Stage IV. f traces of these intestinal cornua. The cells of the dorsal roof of intestine showed in this region a looser structure, and a line of pigm indicated the region of the outfolding. The cells of the duct and t of the cloaca are histologically very different from each other, so it is for a long time possible to draw a line sharply separating the constituents where they have come in contact.

The pronephric system of tubules presents in this stage quite unif histological characters. I shall therefore describe its typical condit and then consider the modifications that are to be found in certai its regions. The walls of the tubules are very thick, measuring on average about 25 μ in thickness. They accommodate themselves rea to the structures with which they come in contact, becoming thin opposite elevations in neighboring surfaces, and thicker next to sinu The size of the lumen varies greatly. In the segmental duct proper, diameter of the lumen is about 25 μ; it is usually somewhat gre in the region of the convoluted tubules. The walls of the tubules composed of an epithelium, consisting of a single layer of columnar c The radial dimension of the cells in the case of thick walls is appr mately three times their width. Where the plane of the section the wall of a tube tangentially, the cells may be seen to have a pol nal outline. The nuclei invariably occur close to the central lume the tube; each is large, and is usually provided with a single dist nucleolus. The eccentric position of the nuclei is attended wit corresponding distribution of the cell protoplasm. By the picro-car method which I have employed, the yolk spherules take a bright yel stain, and the nucleus a light red. The active protoplasm has a f pink coloration, which, however, is wholly invisible if too much pi acid be left in the preparation. In young cells, where only a sn amount of yolk has been consumed, the delicate tint of the protopl cannot be seen, since all the light passing through the section encoun yellow yolk spherules. As the consumption of the yolk progresses, protoplasmic matrix comes into view. In the wall of the tubules, yolk is crowded to the outer surface of the cell, and a sheet of protopl st becomes visible close to the lumen. It is here also that pigment kes its appearance.

The histological character of special regions now claims our attention. e pronephridia shown in Figures 31 to 33 are all histologically very nilar, but in the case of the gland represented in Figure 34 some table differences occur, which I shall consider later. The somato- ure covering the pronephros is at this stage very thin. Each of the ls composing the membrane is thickest in its central portion, and ers rapidly towards its margins. In the more advanced larvæ, the ls have elongated to such an extent that the peripheral portion is luced to a thin protoplasmic plate, which is nearly devoid of yolk erules. The central mass, on the other hand, contains the nucleus, l nearly all the yolk spherules. The peritoneum is continuous with columnar epithelium of the walls of the tubules at the outer rim the nephrostomes, which have the characteristic form of a funnel. fore reaching the periphery of the funnel, however, the columnar layer omes slightly thinner, and at the rim it tapers rapidly, until it becomes tinuous with the peritoneum (compare Fig. 18 of a younger and Fig. of an older stage). The nephrostomal funnels are always deeply pig- nted. The pigment is most abundant along the incurved surface, but quite dense even up to the rim. It continues for a variable distance o the tubules. In the case of the pronephros, represented in Figure the whole system of tubes was pigmented from the nephrostomes to posterior bend near the beginning of the common trunk. The pig- nt granules are always disposed in a layer along the free surface of the ls. The nephrostomal tubules show in general the typical character, ich I have previously described. The collecting trunk appears to be ite rigid, for I have never seen such a reduction of its lumen due to essure as other tubes exhibit. The calibre of this canal is usually larger n that of the nephrostomal tubules. The portion of the duct which s behind the third nephrostome is nearly straight and of uniform calibre. nerally the lumen is slightly wider, and the wall thinner, than in the phrostomal tubules. In the pronephridia, shown in Figures 31 and , the loop embracing the anterior bend of the common trunk seems have but little rigidity. It follows a tortuous course, and fre- ently the walls are so closely pressed together that the lumen is ally obliterated.

A peculiar modification in the pronephros, represented in Figure 34, s been alluded to. In this case, the common trunk, after proceeding m the level of the third nephrostome for a certain distance forward

along the ventral border of the gland, as in the other embryos, un
goes a change of structure at about the level of the second nephrosto
The lumen there begins to enlarge, and the wall to become thin
Farther forward, the cavity of the tube becomes greatly dilated,
the bounding wall is reduced to a delicate pavement epithelium, hav
the same appearance as the peritoneum covering the pronephros.
tube again contracts shortly before attaining its most anterior bend.
similar dilation also occurs in the following stage, in the descriptio
which I shall again refer to the chamber thus produced and suggest
possible function.

The pronephros at this stage is completely invested in a loosely fitt
capsular membrane. The cells of which this envelope is composed h
become very thin, so that they form a delicate sheet not more than
thick. The nuclei occur in slightly enlarged portions of the cells. T
are rather small, and show a tendency to be flattened in the plane
the layer. At the lower outer angle of the myotome, the caps
membrane is continuous with the myotomal sheath, as in the ear
stage. The capsule covers the pronephros so loosely as to leave ex
sive spaces between the enveloping membrane and the tubules. Th
spaces, together with those between the convoluted tubes, form an
tensive and complicated system of sinuses, which bound the pronep
tubules on every side (compare Fig. 28, belonging to the next older sta
Behind the last nephrostome, a considerable space intervenes between
wall of the capsule and that of the duct. There is thus formed a si
continuous but irregular channel, which accompanies the duct throu
out its entire course; it is also prolonged into the region of the glan
a large ventral sinus, which is triangular in cross section (compare
lower of the spaces marked *sn. sng.* in Fig. 28). This channel is
fundament of the posterior cardinal vein. The course of the vessel
be traced at this stage for a short distance behind the point where
ducts open into the cloaca. There are two veins connected with the
terior end of the pronephros. Of these the ventral one is the larger,
is continuous posteriorly with the cardinal vein. The dorsal vesse
the pronephros also unites with the cardinal vein by means of the sp
between the tubules. After passing forward and leaving the proneph
the ventral vessel proceeds medianwards to empty into the sinus veno
this vessel constituting the ductus Cuvieri. The dorsal vessel of
pronephros can be traced forward into the head. In the somite nex
front of the first nephrostome, it lies between the ganglion nodosum
the myotome. It can be traced for some distance along the base of

um, passing close to the median wall of the auditory vesicle and the of the eye.[1]

ere are two kinds of cells found within the capsule of the pronephros rning which I have as yet said nothing. Those which are more rous are scattered, of circular outline and of unform size. Each has neral three or four large yolk spherules, and the nuclei are rather

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order to ascertain, if possible, what vein of the adult this vessel represents, it e necessary to describe here its condition in later stages. In the oldest embryos e examined, 8.5 mm. long, the vein runs forward from the pronephros parallel aortic root and its continuation, the carotid artery. The vein is separated the arterial trunk by the ganglia nodosum and faciale. Recalling the earlier on of the vein, it will be seen that it has been transferred from the median to ternal side of the vagus nerve. In an intermediate stage, I have been able to e nerve during its transit through the vein, thus confirming an observation of chenko ('87, pp. 275, 276).

llowing the vein farther forward, it is found to pass immediately ventral to ditory vesicle, directly in front of which it sends a branch around the ganglion e to the side of the cranium. Slightly farther forward the vein divides, its nes passing around the more anterior of two ventral processes of the gan-faciale. The two trunks thus formed separate. One enters the orbit, and can ced to the anterior end of the optic bulb. The other passes below the eye, rsues a nearly straight course to the anterior horn lip.

lescription of the venous system of the adult frog has been given by Gruby nd by Ecker ('64–81). The distribution of the veins which enter the dorsal n of the pronephros corresponds most closely with the internal jugular of these s. From the figures of Goette ('75), however, there can be no doubt that in I have described corresponds to the one which he calls the external jugular. been able to find a vein entering the sinus venosus directly which agrees ac-ly with the inferior jugular of Goette, but I have found none corresponding one he calls the internal jugular. It is stated by Goette (pp. 759, 760) that in named by him external jugular receives large branches from the maxillary andibular regions. This character would seem to connect it with the exter-gular of Gruby and Ecker. According to Goette (p. 765), however, the exter-gular of Gruby and Ecker is the same as his inferior jugular. I believe this ent to be true, and it seems possible that Goette, who confesses that his studies the veins did not extend beyond the first larval periods, may have erred in count of the distribution of these rudimentary vessels.

ce the preceding description was written, a paper by Marshall and Bles has appeared, which adds another to the divergent accounts I have re-l. The inferior jugular of Marshall and Bles corresponds closely with the have alluded to under that name. The anterior cardinal vein is described by authors ('90^b, p. 236) as "formed by the union behind the ear of a jugular eturning blood from the brain and dorsal part of the head, and a facial vein lies superficially along the side of the head ventral to both eye and ear." vessels are described in tadpoles, measuring 9 mm. in length. My own ations on larvæ of nearly this size do not agree with this description.

smaller than in the cells of the tubules. Very similar elements a in the fundaments of blood-vessels at this stage, and it is eviden the cells are embryonic blood corpuscles. The spaces in which occur constitute a complicated system of communicating blood si and are continuous with the lumens of the vessels entering and l the pronephros.

The other class of cells to which I have referred are mesenchy I have carefully studied these cells in the endeavor to ascertai precise origin. A mode of reasoning similar to that employed cussing the probable origin of the inner cells of the glomus le the conclusion that the mesenchymatic cells of the pronephros have been given off from the walls of the tubules. As I have the cells in these walls are very thick, and their nuclei lie close lumen of the tube. Under these circumstances, it is difficult to stand how any cells of the tubule should divide so as to give of their basal surfaces cells as small as those in question. The usu cess of cell division, if it took place parallel to the surface of the would result in the production of a small cell on the side towa lumen and a large outer segment. Such a large cell might, it is by repeated divisions, break up into numerous small cells, but for s reasons I do not believe this to have been the case. If such a dela tion and subsequent cell division took place, it would naturally conspicuous process; but I have never observed any evidences This method of origin would involve a considerable thinning of the which does not take place.

There remain two other possible sources for the mesenchymatic of the pronephros. They may have arisen from the tissue bou the pronephros, viz. the capsular membrane and the adjacent so pleure, or they may have come from remote regions. In ju between these possibilities, it is important to consider the s appearance of the cells and the small amount of differentiation have undergone. It seems to me highly improbable that they s have already accomplished any extensive migrations. Under thes cumstances, such positive evidence as I am able to adduce is the convincing. In studying the youngest stages in which mesenc was present in the pronephros, this tissue was usually found nea somatopleure or the capsule, and frequently consisted of a row of closely applied to one of these layers. Occasionally I have seen a of mesenchymatic cells arranged along the somatopleure in a very de manner, so that the nuclei of the two layers lay directly opposite r and the intercellular regions precisely corresponded. In such the evidence seems strongly in favor of delamination, but I have r seen a nucleus dividing in that direction. This negative evi- e, however, should have little weight, since all cell divisions occupy nparatively short time, and are also obscured by the numerous yolk rules. The observations just recorded agree very well with the thinning of the somatopleure to which I alluded in discussing the logy of the tubules. I conclude, then, that the mesenchymatic tissue e pronephros arises from the adjacent somatopleure, and probably o some extent from the capsular membrane.

e glomus (Plate I. Fig. 10) has attained in this stage nearly its final nsions. The lateral plate having become wholly detached from the vertebræ, the glomus has the appearance of being attached to the wall e body cavity at its dorsal angle (compare Fig. 9, of a younger stage, ig. 47, of Bufo). There is some individual variation, but in general y be stated that the ridge constituting the organ under consideration ds continuously from the first nephrostome backward to a position ly behind the third. It appears in cross section (Fig. 10) obovate, attached by the narrower end. In structure it is very compact, at it is difficult to locate with precision cell boundaries in the dense or mass. The investing portion consists of a single layer of cells, is continuous with the peritoneum. These cells are large, and the form of spheres flattened on their inner surfaces (compare Plate igs. 49 and 50, *la. pi'ton.*, which represent this layer in Bufo). They ightly pigmented, and a distinct row of pigment granules can usually en close to the inner surface of the layer. These outer cells are ntly the representatives of the large cells of the splanchnopleure was folded, at a previous stage (see page 227), to form the earliest ment of the glomus (Fig. 9, *fnd. glm.*). In certain favorable re- I have seen a thin structureless membrane lying directly within the cellular layer (compare Figs. 49, 50, *mb. ba.*). When any of the of that layer become detached, which frequently happens, this base- membrane usually remains in place, and gives a sharp outer con- to the glomus in that region. Besides the compact mass of large there occur within the organ one or two cells in each section (com- Figs. 49, 50, *en'th.*) which have an elongated form. They lie close e basement membrane, with which their long axes are parallel. In ns each cell has a central swollen portion containing the nucleus, which it tapers in both directions. I have not been able to trace lelicate lateral portions to their terminations, but I believe that

these cells form a complete endothelial lining, which follows close
delicate basement membrane. They doubtless represent the loos
alluded to in Stage IV. as occurring within the fundament of the gl
Their origin I have already discussed in connection with that
where I showed that they were probably not derived from the
layer of the glomus. Although the structure of the central m
cells is, it must be admitted, somewhat obscure, I have found n
dences of the complication which Hoffmann ('86, p. 591) has re
maintained for it.

On the contrary, a comparison of many individual cells in this
with the loose cells in the cavity of the aorta has made me con
that most of the cells contained in the glomus are embryonic bloo
puscles. It is possible, however, that others are derived from in
portions of the outer layer of the glomus. They appear to ha
representatives in early stages of the organ. In my opinion, the
glomus is essentially a blood sinus, the wall of which projects in
body cavity, carrying before it the peritoneal layer.

The junction of the two aortic roots takes place very nearly op
the first nephrostome (compare Plate IV. Fig. 28, *rx. ao.*). The
trunk thus formed (Fig. 10, *ao.*), since it occupies the space betwe
chorda and mesentery, passes close to the attachment of each glom

The precise relations of the aorta to the glomus are rather diffic
observe, since the former is peculiarly liable to injury in secti
The interior of the chorda at this stage consists of a frail vesicular
whereas its outer sheath is tough, and resistant to cutting instru
In sectioning, therefore, it collapses, and occasions serious distort
the adjacent parts.

In the younger individuals of this stage, the cavity of the aor
not seem to be sharply marked off from the root of the glomus; in
eral instances, indeed, I was able to observe a continuity betwee
endothelium of the aorta and that lining the glomus. In older
viduals I have repeatedly noticed distinct branches from the aorta
ing into the glomus (Plate I. Fig. 10, *va. sng.*). These observ
were made, however, only on the most favorable sections, and I
been unable to ascertain the number or distribution of such bra
In both of the two most obvious cases, however, the vessel entere
hinder end of the glomus. Occasionally, the vessel to the glomus
to be only a lateral branch given off from a vessel which can be
between entoderm and splanchnopleure for some distance ventral
glomus (Fig. 10, *va. sng.*, the lower of the two dotted lines).

ave spoken of the expanded dorsal portion of the body cavity, into
h the nephrostomes open, and which contains the glomus. This
on of the body cavity constitutes the so-called pronephric chamber.
not to be regarded as a closed cavity. Elsewhere the somatopleure
the splanchnopleure are closely applied to each other, but there is
utely no fusion of these layers ventral to the pronephros.

STAGE VI.

late III. Fig. 27. Plate IV. Figs. 28, 30, 35-38, 41. Plate VI. Fig. 51.

e larvæ included in this stage are in general two or three days
than those of the preceding stage. They are about 8 mm. long
the anterior end to the tip of the tail. In this stage, the body no
r tapers gradually from the branchial region to the posterior end;
a definite line of separation is established between the trunk and
egions. In the tail a distinct membranous fin has appeared, both
; the dorsal and the ventral median lines. The horn lips can be
surrounding the mouth, and the external gills project prominently
th sides of the body.

e pronephros of this stage has developed along lines foreshadowed
e preceding stage. The general form of the organ can best be un-
ood by reference to the series of diagrams (Figs. 35–37) and the
struction (Fig. 41) given on Plate IV. As will be evident at once,
land has reached a high degree of complexity, produced, however,
continuation of the same process of complication which had begun
age V. Thus the first nephrostomal tubule[1] and the collecting
retain throughout a nearly unmodified condition; the third ne-
tomal tubule usually becomes slightly complicated; the second
its the greatest number of convolutions. The common trunk,
ver, is the part which has been principally concerned in producing
ncreased complexity of the gland. It is to be noted that this con-
on is not of a wholly indefinite nature; indeed, there is consider-
uniformity in the pronephridia of different individuals of the same
of development. In Figure 31, representing a pronephros of a
in Stage V., it is to be seen that there are only two bends in the
non trunk, which extends forward to the anterior end of the gland.
this simple condition the later complications may be derived by a
imple steps. In order to follow the changes it will be advisable to

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The same colors have been employed for corresponding parts in both Figures
d 41. Consult explanation of Figure 41.

distinguish: (1) posterior bend adjacent to the collecting trunk, (2 cending arm, (3) anterior bend, and (4) the descending arm, whic continuous with the segmental duct. The simplest condition wh have found in Stage VI. is represented in Figure 35. This dia relates to a larva of R. sylvatica Le C., and it is of interest to no close similarity to Figure 38, which represents the pronephros larva of R. pipiens Schreb. (halecina) of this stage. These two nephridia will be considered together. In both, the ascending ar the common trunk makes either an S-shaped bend or a loop int lated near the middle of its course; the transverse portion, or ant bend, is thrown into one or two slight folds, and the descending shows two loops, one in the middle of the gland, and the other its posterior end. The two remaining diagrams (Figs. 36, 37), th taken from different individuals, are alike in all essential particu The principal changes from the condition shown in the simpler p phridia just described consist in the development of an additional in the course of the ascending limb, and of several slight folds in transverse portion; the loops present in the younger individuals of stage have persisted and become more extensive. In the case of larva whose pronephros is represented in Figure 37, I made a con ative study of the pronephridia found on the two sides of the b The comparison showed that a slight want of symmetry existed bet the two sides. Occasionally the direction in which equivalent t were bent did not correspond. On the right side of the body (the figured), for example, the hindermost loop of the descending arm formed by an inward bend, while in the left pronephros the correspon tube is bent outward. In the descending arm of the left pronephr small loop occurs in addition to those present on the right, while or the two loops occurring in the ascending portion of the right sid almost unrepresented on the left; thus, the right pronephros app mates in this respect the simpler organ represented in Figure 35. more striking anomaly of the left pronephros consists in the occurr of a slight bend of the collecting trunk between the junctions of the ond and third nephrostomal tubules, so that the latter connects with ascending portion of the collecting trunk. Finally, the third nep stomal tubule of the left side joins the collecting trunk farther pos orly than does the one on the right side. In general, however, it se to me that the several pronephridia studied show a rather remark uniformity even in the details of the arrangement of their tubules.

The position of the pronephros with reference to the muscle plat same in this stage as in the foregoing. The lateral plate is now olly cut off from the myotomes; but a study of serial sections shows t each nephrostome lies beneath a myotome. These myotomes correond to somites II., III., and IV.

The course of the duct in this stage is the same as in Stage V. The enings into the cloaca (Plate III. Fig. 27, *dt. sg.*) are now situated at bottom of a depression in the dorsal wall of the cloaca (*clc.*). While excretory products enter the main cloacal chamber by a single aperre, a glance at the histological characters of the short median unpaired nk shows that it is lined with entodermal cells, and is therefore really diverticulum of the roof of the cloaca. The ducts of the two sides, refore, are not to be regarded as uniting into a common trunk, but opening separately into a dorsal diverticulum of the cloaca.

The histological characters of the pronephric system have not underne any great changes since the preceding stage. Figure 28 (Plate IV.) ws a cross section of the left pronephros of the larva, whose right nephros is diagrammatically represented in Figure 37. The plane the section passes through the first nephrostome, and the transition m the pavement cells of the peritoneum to the columnar epithelium the tubules is clearly shown. This section also shows, besides the t nephrostomal tubule, the anterior ends of two loops which belong the transverse portion of the common trunk. The walls of all the ules are thinner than in the preceding stage, and since the nuclei rein of about the same size as heretofore, they now occupy a far larger portion of the cell, and in the case of the thinnest-walled tubules are quently almost in contact with both the outer and inner surfaces of cell. The amount of yolk in the cells is considerably lessened, ecially in those parts which exhibit the greatest number of convoluns. In some cells, a single large spherule is the sole remnant of the merly abundant yolk. Pigment is present as scattered grains in the lls of all the tubules; it also shows a tendency, as in the previous ge, to accumulate along the free surfaces of the cells. The nephromes, however, are densely pigmented on the surface that is directed vards the body cavity and the lumen of the tubule. The duct posior to the pronephros (Fig. 30) offers no features worthy of special ntion. It is accompanied throughout by the cardinal vein (*vn. crd.*), the median side of which the earliest fundaments of the mesonephric ules are visible.

I have described a special enlarged region of the convoluted duct in arva of Stage V. A similar condition is apparent on both sides of the body in the case of the individual whose pronephros is represented in Figure 35. The dilated chamber (Plate VI. Fig. 51) is here formed by a great expansion of that portion of the ascending arm of the common trunk (*trn. com.*) which is adjacent to the collecting trunk (*trn. clg.*). A similar dilated chamber occurs in the pronephros represented in Figures 36 and 41; but in the latter case neither the dilation of the lumen nor the thinning of the wall is very pronounced. In both these cases the expanded chamber is present in portions of the tubular system which are exactly equivalent to each other. Under these circumstances, the expansion of the *descending* limb of the duct occurring in the pronephros of Stage V. (Fig. 34) seems quite anomalous. The dilated chamber is invariably, however, superficial in position, lying close to the capsular membrane. I have been unable to reach an entirely satisfactory opinion regarding its function. Since it is situated so near to the nephrostomes, it does not seem very well adapted to serve as a reservoir for the storage of fluids secreted by the gland, for by far the larger portion of the secreting surface is situated between it and the duct. However, the chamber doubtless receives whatever fluids are gathered by the nephrostomes or are secreted by the peritoneal tubules, and it is possible that the enlargement exists solely for this purpose. In following the duct from the dilated region towards its outlet, a greatly contracted portion is reached, and this may serve for the better retention of fluid contained in the chamber.

The capsule in these larvæ is not so well marked as in those of the preceding stage. Between the pronephric tubules and the ectoderm there has arisen a considerable quantity of mesenchyme, and the capsule now appears merely as the line along which this mesenchyme comes in contact with the pronephric tubes and blood sinuses.

In discussing the blood supply for the preceding stage, it seemed advisable to consider the vessels in older larvæ as well, and I shall therefore merely refer here to the account given in that connection.[1]

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[1] In all the larvæ of this stage which I have examined, I have observed a peculiar sac, of which I have been unable to find any mention in the literature. In the oldest larva of this stage it consists of a capacious sinus lying in the triangular area bounded by the myotomes, the somatic peritoneum, and the ectoderm. It extends backwards from the niveau of the third nephrostome for a length of two or three myotomes, and appears to be closed upon all sides. The sac lies in a mass of loose mesenchyme, but possesses firm walls, so that any opening would naturally be easily recognizable. In the interior of the sac, cells which are undistinguishable from blood corpuscles are found in considerable numbers. In a younger larva the sac occurs in a corresponding position, is nearly filled with blood cells, and is in open

he glomus is somewhat larger and more compact than in the preced-
stage, and for that reason its structure is more obscure; but I have
nothing which would lead me to believe that it differs materially
the condition exhibited by the younger glomi of Stage V. The
n is bounded by a definite peritoneal layer and contains blood cells
ther with embryonic connective-tissue stroma. The blood cells are
lly contained in definite channels, and, being closely packed together,
uently appear in cross sections to be disposed with considerable reg-
ity around a central point. This arrangement is naturally suggest-
of a tubular or a rod-like structure; but the histological characters
e cells and the conditions exhibited by adjacent sections show that
impression is illusory. In short, I have been unable to find within
glomus any traces of the rods and thick-walled tubes which have
described by Hoffmann ('86, p. 591).

o closed pronephric chamber exists at this stage. In the most
rior sections in which the pronephric tubules appear, a blind anterior
rticulum of the body cavity is to be seen; but this unites with the
ral body cavity surrounding the intestine even before the niveau
e first nephrostome is passed. Throughout the remainder of the
ephric region the lung bud (Plate IV. Fig. 28, *fnd. pul.*) forms a
on the splanchnic side of the cœlom. This ridge partially separates
pronephric chamber from the general body cavity; and in the region
e third nephrostome a still more perfect closure is effected on the
side of the body by means of the approximation of a portion of the
ut to the peritoneum covering the pronephros.

STAGE VII.

he age of the larvæ of this stage, reckoned from the time of fertiliza-
is about forty-seven days. A large gap therefore intervenes between
es VI. and VII., and the older larvæ are studied merely for the pur-
of observing the process of degeneration in the pronephros. In the
of Stage VII. the mesonephros has already attained a degree of
plication comparable to that gained by the pronephros at Stage VI.,
the same average number of tubes appear in cross sections through
two glands. The mass of contorted tubules in the case of the meso-
ros, however, is formed wholly by the transverse tubules, while the

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unication with the cardinal vein. In a larva of intermediate age, the sinus
unicates with the cardinal vein by means of a very narrow canal. Respect-
he fate and the significance of this singular structure, I have no suggestions to

duct pursues a direct course through the gland. The duct is situa
in the dorsal portion of the mesonephros adjacent to the lower bord
of the myotomes; its relations are therefore different from those of t
longitudinal canal of the pronephros, since, as we have seen, the comm
trunk in the pronephros is greatly convoluted, and its windings occu
the ventral portions of the gland.

The marked signs of degeneration which the pronephros presents
this stage prevented my reconstructing the gland, since it proved to
impossible to follow any given tube throughout the entire series of s
tions. Indeed, I am convinced that the tubules are no longer stric
continuous. I must therefore content myself with a brief descripti
of the histological features noticed.

The lumen of the tubules is greatly enlarged, and is frequently fill
with a dense coagulum which stains similarly to protoplasm. The c
walls are very thin and show a tendency to become shredded or fray
along the interior surface. The membranes between the cells in t
wall have become indistinct, and the number of nuclei in a given ar
is far less than in a corresponding portion of the wall in Stage VI. T
nuclei are stained only feebly, but contain deeply staining granules, a
seem to be disappearing, since one can observe numerous gradatio
between the typical nuclei and those which have become so pale as
be nearly invisible. The ground substance of the walls is slightly vac
olated and contains numerous scattered dark granules. Between th
remnant of the cellular wall of the tube and the basement membran
I have frequently seen small cells with deeply stained nuclei. The
may possibly represent intrusive connective-tissue elements.

I regret that I have not been able to make an extended study of t
degeneration of the pronephros; but the limit which I have set to m
work is perhaps the least arbitrary which I could easily make.

B. Bufo.

The development of the pronephros and the segmental duct in Bufo
very similar to that which I have described for Rana. For this reaso
I can treat the development in Bufo much more briefly, and shall l
principal stress upon those features which are unlike in the two genera

STAGE I.

In the case of Rana, this stage included embryos which showed an
defined somatopleural thickening lying immediately posterior to t
cranial ganglionic mass. This proliferation proved, on comparison wi

der specimens, to be the first indication of the pronephric thickening.
similar condition of the somatopleure is presented by embryos of Bufo
out 2 mm. long, in which the medullary folds are widely open.

The general relations of the germinal layers at this stage are almost
entical with those in Rana, and the same histological criteria for distin-
iishing them can be employed. The ectoderm is very sharply marked
f from the mesoderm. The former is deeply pigmented, while the ad-
cent mesoderm is almost destitute of pigment. The yolk spherules
the ectoderm measure on the average about 2 μ; those of the meso-
rm, about 4 μ.

In embryos in which the medullary tube is still widely open, the
matopleure and splanchnopleure are separated from each other by a
stinct space, the cœlom, which can be traced with perfect distinct-
ss into the protovertebral plate, where it becomes slightly expanded.
the anterior half of the embryo, both the somatic and the splanch-
c layers are only one cell in thickness. Posteriorly, and in the middle
unk region, however, certain loose cells bordering on the cœlom become
sociated with the somatic layer; but this layer is never, except at the
treme hinder end, more than two cells in thickness.

STAGE II.

Embryos in which the medullary tube is just closed exhibit a con-
tion of the mesoderm slightly different from that of Stage I. In the
sterior portion of the embryo, the mesoderm is quite thick in the re-
on of the protovertebral plate, and becomes gradually thinner as it
proaches the ventral portion of the body.

Anteriorly, the protovertebral plate shows traces of the differentiation
four or five protovertebræ. Of these, the most anterior lies in the same
ansverse plane as the ganglion nodosum, and, following the method of
signation which was employed in the case of Rana, would properly
present somite I. This protovertebra, as in Rana, shows signs of
ansformation into mesenchyme, and is considerably compressed in the
gion of the ganglion.

The thickening has the general form which I have described for the
rresponding stage of Rana, and its anterior margin is situated under
mite II.

In the region of its greatest thickness, which is somewhat lateral to the
undary between the protovertebra and the lateral plate, it is two or
ree cells deep. It thins out slowly on the ventral side, much more
pidly on the side of the protovertebra, or dorsally. The thickening

involves the ventral portion of the lateral wall of the protovertebra itsel although the greater part of the thickening is in the region of the latera plate. I have not been able to find any sharp plane of division markin the lower limit of the thickening. The latter extends posteriorly throug a distance of three or four somites, but it is difficult to make out its relations to the protovertebræ, in consequence of the small amount of differentiation which these exhibit at this stage. It seems to me, however that the thickening reaches backward into a region posterior to tha in which the pronephric tubules later develop, and therefore represent already the first fundament of both the pronephros and the anterior en of the segmental duct.

Frontal sections show the same relations between the pronephri thickening and the protovertebræ that I have described for Rana, bu in Bufo the cœlom is entirely obliterated by the growth of the pronephric thickening, and consequently the pronephric chamber described i a corresponding stage of Rana does not exist in Bufo. This circumstanc renders the determination of the precise boundaries between the two layers of mesoderm somewhat more difficult in the Toad than in the Frog but still there is usually an unmistakable line of division between somatopleure and splanchnopleure even in the former. The pronephric thickening at this stage is from two to three cells thick, and is a soli mass.

STAGE III.

In embryos of this stage, the fundament of a single pair of gill-folds is present; the fundament of the auditory vesicle consists of a simple thickening, which is just beginning to separate from the superficial ectoderm; and five or six protovertebræ have made their appearance. The embryos measure from 2.25 to 2.50 mm. in length.

The pronephric thickening becomes sharply marked off in this stage from the undifferentiated mesoderm lying ventral to it, and the canalization of the structure is accomplished by the arrangement of the cells around a lumen. Segmentally, the pronephric thickening has in general the form of a close fold of somatopleure, whereas intersegmentally it appears as a flattened tube. The points of continuity with the cœlom are situated each directly beneath the middle of a protovertebra, and the somites in which they appear are II., III., and IV.

The duct arises as a backward continuation of the pronephric thickening, and contrasts very sharply in histological characters with the ectoderm, in consequence of the pigmentation and paucity of yolk spherules in the latter.

STAGE IV.

Plate V. Fig. 43.

Embryos of this stage measure from 2.8 to 3.1 mm. in total length. luscular fibres have begun to appear in the myotomes, the auditory esicles are entirely detached from the external ectoderm, and the pro-vertebræ have been differentiated as far back as the anus.

The pronephric pouch of Bufo is very similar to that of Rana. It ommunicates with the cœlom by means of three nephrostomes, and om its ventral margin the duct takes its origin. The nephrostomes e segmental in position, and are situated beneath protovertebræ II., II., and IV.[1]

The duct can be followed for some distance posterior to the hinder-ost pronephric nephrostome as a distinct elliptical tube with a central imen. The lumen, however, disappears further posteriorly, and the uct terminates either as a simple thickening of the somatopleure, or its osterior end merely rests upon the mesoderm in the region of somite I. The hinder tip of the duct (Fig. 43, *fnd. dt. sg.*) in both cases re-embles very closely the adjacent mesoderm both in the size and in the oundance of yolk spherules, and it differs from the ectoderm both in ese features and in the scarcity of pigment. In Bufo I have never een so fortunate as to find the growing end of the duct situated in a roove of depressed mesoderm; but I believe that the fundament ex-ends itself from the region of its origin in the somatopleure to the pro-ecting cornu of the cloaca by means of an independent growth on the art of its own cells. The greater part of the duct, however, arises from local proliferation of somatopleure.

The pronephric capsule in Bufo arises as a downgrowth from the outer eripheral layer of the protovertebræ. In this stage, however, it has not eached the somatopleure ventral to the pronephros, but merely forms a vo-layered scale-like sheet of tissue covering the dorsal portion of the land.

The pronephric chamber is present at this stage. The general body avity, however, has not yet appeared, the somatopleure and splanchno-leure being in other regions in close contact.

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[1] I have preserved in the enumeration of the body somites of Bufo the same esignations that were employed in the case of Rana. In Bufo, however, the ker-el of the degenerate protovertebra in front of somite I. gives rise to a few muscle ores.

Stage V.

Plate V. Figs. 42, 46. Plate VI. Figs. 47, 49, 52.

At this stage the larvæ were hatched and swam about freely in aquaria. The larvæ measured from 4 to 6 mm. in length, and each h a distinct tail, which protruded for a distance of 1.5 to 2 mm. beh the anus. The pronephros was probably already functional.

The character of the convolutions of the pronephric tubules studied in the case of four pronephridia. In this feature one of th corresponded very closely with the condition in the pronephros of Ra represented in Figure 33. The remaining pronephridia differed fr this type solely in the circumstance that the third nephrostomal tub joined the collecting trunk at the extreme posterior portion of the be which in Rana usually forms the first portion of the common trunk.

The position of the pronephros with reference to the somites rema in general nearly the same as in the preceding stage. In individ cases, however, the nephrostomes do not appear to lie precisely under middle of the myotome.

In embryos of this stage, the segmental ducts already open into cloaca. These openings are situated beneath myotome XII. It obvious from this fact that the duct in the older embryos of Stage had already very nearly reached the region of its final communicati with the cloaca. In Bufo the lumen of the gut is very narrow, and is s arated from the lateral walls of the body by an extensive mass of yolk ce The cloacal cornua are therefore in this case very long, extending to outer surface of the entoderm. The ducts reach these cornua by passi between the dorsal angle of the body cavity and the overlying myotom

The histology of the pronephros in Bufo does not present any no worthy features of difference from that in Rana. The tubes are slightly smaller in Bufo, and their walls contain somewhat more pigme than do those of Rana.

The capsule envelops the pronephros and duct in the way that I ha described for Rana, and it also encloses a series of blood sinuses whi are developed from the posterior cardinal vein. I was not able to obta in Bufo any additional evidence in regard to the origin of the mesenchy of the pronephros.

Two veins emerge from the anterior end of the pronephros. One these is the immediate continuation of the posterior cardinal vein, whic in passing forward as the ductus Cuvieri (Plate V. Fig. 42, *dt. Cu* makes a rapid ventral descent to open into the sinus venosus. T ıer vein (Fig. 42, *vn. jgl.*) passes forward between the myotome and vagus nerve. It evidently is one of the jugular veins, but I have been able to study its distribution in later stages, and am therefore ıble to state more precisely which vein of the adult it represents.

The structure of the glomus in Bufo is far more evident than in corponding stages of Rana. In treating of the development of the glos in the latter, I reached the conclusion that it arises as a simple l of splanchnopleure, into which mesenchymatic cells migrate. In r stages I was able to identify the original outer sheath with a tinct basement membrane, and found within this membrane a large nber of embryonic blood corpuscles, and occasionally certain cells ch resembled in their histological characters those of the sheath or itoneal layer. In Bufo the vascular system is less developed than in corresponding stage of Rana; and, owing to the small number of the od corpuscles, the remaining cellular elements come more plainly into v. The usual form of the glomus is that of a hollow peritoneal sac d with endothelium (Plate VI. Figs. 47, 49, 50), and containing scatd blood corpuscles (Fig. 46). At the entrance to the sac the endolium (*en'th.*) is continuous with the loose mesenchyme surrounding aorta, and, in certain regions, the lumen of the latter can be traced the interior of the glomus. This organ, then, exhibits markedly character of a blood sinus, the walls of which project into the body ity. Occasionally one encounters in Bufo certain minor pocketings of peritoneal layer of the glomus, — invaginations into the lumen of glomus at the place, e. g., occupied by the letters *cœl.″* (Fig. 52). he cells at the apices of such invaginations were to become detached, condition would serve to indicate the source of the pigmented cells ıd in the interior of the glomus in the case of Rana, although I have ret reached no final conclusion in regard to this matter.

n this stage the body cavity exists as a distinct lumen only in the on from which the nephrostomes emerge, where it constitutes a prohric chamber.

Iy studies on the development of the excretory organs in Bufo have extended beyond the present stage.

C. Amblystoma.

Plate V. Fig. 44. Plate VI. Fig. 48. Plate VII. Figs. 53-56. Plate VIII. Figs. 57-65.

ımblystoma shows in the development of its excretory system many tures of similarity to the Anuran forms already described. The differences, however, are far greater than those which exist between Ra and Bufo, and will require for their presentation a fuller treatment th was given in the case of the latter genus; but the development in three genera is sufficiently similar to allow the recognition of the sar successive stages, based upon the degree of complication exhibited the pronephros.

STAGE I.

Plate VI. Fig. 48.

In embryos of this stage, the two lateral medullary folds have ju fused to form the neural tube. The embryos have a slightly elongat form and measure about 3.7 mm. in length. They are slightly mo advanced than the embryo of Amblystoma represented by Bambe ('80, Planche XI. Fig. 35). The eggs from which I derived my seri of embryos had been deposited for a variable length of time before th were collected, and I am unable to give the ages of the several stages.[1]

The general arrangement of the germ layers (Plate VI. Fig. 48) similar to that which I have described for Rana and Bufo. The ect derm (*ec'drm.*) consists in general of a single layer of cells, each of whi has the form of a cube slightly flattened. Scattered ectodermal ce form an incomplete deep layer, which may gain in some regions, e. g. the head, a very considerable development. The outer face of ea ectodermal cell possesses a thin layer of pigment, but this is by no mea so dense as in Rana and Bufo. At this stage yolk spherules are abu dant in all the cells of the ectoderm.

The entoderm has nearly the same arrangement as in Rana, but t yolk cells are relatively more abundant, and the lumen of the gut narrower. In the anterior region, the chorda consists of a simple fold the dorsal roof of the intestine; but in the posterior portion of the bo it is represented by a single row of high columnar cells, which form layer convex from side to side towards the lumen of the intestine. Th layer is the one which O. Hertwig ('83) has named the chorda-ent blast. The cells of the yolk entoderm are in general the largest in t

[1] A quantity of the eggs of Amblystoma punctatum Linn. raised in the laborato during the present season reached the several stages as follows: Stage I., 5 day Stage II., 5 days, 12 hours; Stage III., 6 days, 15 hours; Stage IV., 7 days, hours; Stage V., 8–14 days; Stage VI., 15–20 days. These figures are only appro imate, and between Stages II. and V. the individual variation is frequently mo than sufficient to cover the entire interval between two successive stages. Th temperature of the water varied somewhat during the period, but I believe th 10 or 11° C. would be a fair average.

, and contain very large yolk spherules. The majority of the ento-al cells contain no conspicuous accumulations of pigment; but the r may occasionally be found in considerable quantity, particularly in ells bordering on the gut.

the dorsal portion of the body, the mesoderm consists of two lateral es of tissue, each of which spreads outward and ventralward from neural tube, and joins its fellow of the opposite side in the ventral an line. Each of these masses of mesoderm is thickest next to nedullary tube, and gradually becomes thinner in passing outward nd the mass of yolk cells. In the dorsal half of the body (Fig. 48) mass of cells consists of two distinct layers, which are continuous each other along the sides of the neural tube. They represent the division into somatic (*la. so.*) and splanchnic (*la. spl.*) mesoderm, and light space which separates them is the cœlom (*cœl.*). On passing ard and ventrally, the two layers of mesoderm gradually approach, at length are continuous with, each other; for a short distance er, it is still possible to trace two rows of nuclei, indicating approx-ely the territory occupied by the layers; but this arrangement y disappears, and before the ventral surface is reached the meso- has the form of a layer only one cell in thickness (*ms'drm.*).

both somatic and splanchnic layers, the cells are of a nearly cubical , but those of the parietal layer are rather thicker, and may be even nnar. The mesoderm of the ventral side of the body, on the other , is composed of more flattened elements. The cells of the meso- are in general intermediate in size between those of the ectoderm of the entoderm. Their yolk spherules are much smaller than those ne entoderm, but resemble those in the ectoderm too closely to af- a thoroughly satisfactory criterion for distinguishing the two layers. mesodermal yolk spherules are, however, *slightly* larger than those of ctoderm; and in doubtful cases they may be taken into account.

e pigment of the mesoderm is usually collected along that surface e cell which faces the cœlom, and may in part serve as a guide for ving that cavity in cases where the bounding layers of mesoderm are se contact with each other.

ave spoken of the somatic mesoderm as a layer a single cell in ness; this is not, however, an adequate representation of the actual ition. In many sections there may be observed, from place to place, dditional cell associated with the otherwise single layer. The occur- of an incomplete second layer of cells is most noticeable in the rior portion of the trunk, in a region directly lateral to the protover-

tebral plate. It is probable that this slightly thickened somatic la
is the first indication of the pronephric thickening.

Stage II.

Plate V. Fig. 44.

Embryos of this stage measure nearly 4 mm. in length ; the mec
lary tube has become entirely separated from the superficial ectode
and three protovertebræ can be distinguished in longitudinal sections

The fundament of the pronephros forms in this stage (Plate V. Fig.
an evident thickening of the somatic mesoderm lying immediately late
to the protovertebral plate. Throughout the greater part of the thi
ening, the layer is obviously two cells thick, and occasionally three nu
may be seen in a line perpendicular to its surface. The cells constit
ing the thickening are closely compacted, and do not appear to fo
definite layers. The fact that the thickening passes through a stage
which it is only two cells in thickness precludes the possibility of
being a disguised fold with closely applied walls, for in that event th
must be at least three layers of cells involved. Neither the anterior
the posterior limit of the thickening can be clearly determined at t
stage. I am also unable to state definitely its relations to the protov
tebræ, inasmuch as these cannot be adequately made out in transve
sections, and the extent of the thickening cannot be satisfactorily
served in such longitudinal sections as pass through both the protov
tebræ and the pronephric thickening. The latter may be traced fo
distance of about 0.5 or 0.6 mm. Each protovertebra at this st
measures about 0.27 mm. in length, so that the thickening exte
through a length of about two protovertebræ.

In slightly older embryos the pronephric thickening becomes in g
eral three cells in thickness ; but it is still a solid proliferation, with
indication of extensions of the cœlom between the layers.

Stage III.

Plate VII. Figs. 55, 56.

At this stage the young Amblystomas are about 4.3 mm. long and
tinctly elongated in shape ; but they show as yet no trace of a t
They are further characterized by the possession of about eight v
marked protovertebræ.

In all the embryos of this stage the pronephric thickening is at le
three cells in depth, and has a definite ventral boundary. The thicken
extends as far forward as the front face of somite III., and posterio

rs gradually into undifferentiated somatopleure. The backward pro- ation of the thickening is the first fundament of the segmental duct, may be traced at least as far back as somite VI. Both portions of thickening appear to arise in the same way; namely, by cell prolifer- 1 in the somatopleure.

is a matter of some difficulty to ascertain when the first trace of a en appears. Before the two walls actually separate, the nuclei fre- ntly show an arrangement which is suggestive of an evagination; one cannot always trust such appearances. Later, a line of pigment be traced from the body cavity for some distance into the interior of hickening, and finally the two walls separate, leaving a clearly defined en. In all cases, the two regions of continuity with the cœlom are site the middle of protovertebræ III. and IV. respectively; and e is no indication whatever of a continuous fold.

lthough the pronephric mass thus shows evident signs of segmen- on, yet, as is to be seen by a comparison of segmental and interseg- tal regions (Plate VII. Figs. 55 and 56), the proliferation is not rupted in the latter regions. In frontal sections through prone- dia in which a definite lumen has begun to appear (compare Plate Fig. 55), there can be seen two narrow canals leading from the ties of protovertebræ III. and IV. and extending outward as cœlomic rticula into the pronephric mass. From this condition the hasty lusion might be drawn that the narrow canals are in fact outgrowths the *protovertebral* cavities. This however, in my opinion, is not the . If the relations of the mesoderm in such a transverse section as is n in Figure 55 be regarded, it will be seen that a frontal section ugh the pronephric region (in the figure cited, a horizontal section a e below the level of the letters *cœl.'*) would cut through the proto- ebral cavity near its floor, and at the same time pass through the en of the pronephric thickening. Since, moreover, these two spaces continuous by means of the communicating canal, it might at first ar that the latter belonged to the pronephric tubule. The fate of portion of the tube, however, shows this interpretation to be incor- , and that it was only by means of the communicating canal that the en of the pronephros communicated with the protovertebral cavity; vhen the separation of the protovertebræ from the lateral plate takes e, the communicating canal, which is assumed to be the stalk of the ephric diverticulum of the protovertebra, becomes closed, and the ephros is thereby left in communication with the body cavity alone npare Mollier, '90, Taf. XII. Figs. 10 *c.*, 10 *d.*, tr_1 and tr_2).

STAGE IV.

Larvæ of Amblystoma do not possess a conspicuous widely pronephric pouch, such as has been described in Anuran species the proliferation becomes at once converted into a tubular organ. deed, the condition of the pronephric thickening in Stage III. is the which is most similar to the Anuran pronephric pouch, since it is a continuous structure having connections with the cœlom in segm regions.

In slightly older embryos, the dorsal half of the pronephric thic ing is no longer continuous through the region between protovert III. and IV.; and from this region backward to the hinder face of tovertebra IV. the mass is distinctly divided into two tubes. Of two tubes, the more median and dorsal is the second nephrost tubule; the more lateral and ventral is the common trunk. Fir it is to be observed in a number of cases that an anterior loop of common trunk occurs a short distance in front of the point of junc with the nephrostomal canals. The pronephros thus has a form w approximates very closely to the condition which forms the sta point for the next stage (Plate VIII. Fig. 58).

STAGE V.

Plate VIII. Figs. 57-60.

This stage includes embryos which have attained a length of 5 to 6 mm. Many of the older embryos of the stage have alr hatched; they possess well developed tails and swim about freely.

The general form of the pronephros has been studied by means number of rough reconstructions, some of which are represented by diagrams on Plate VIII. In Figures 57 to 60 inclusive, which be to this stage, no windings have been reproduced which were not of ficient magnitude to form definite antero-posterior loops; and, furt in plotting these loops, no attempt has been made to preserve in diagram the natural direction in which the tube is actually bent. H ever, the relative positions of the bends in an antero-posterior direc have been accurately reproduced.

In the younger individuals of this stage, the pronephros (Fig. resembles in many respects that of Rana represented in Figure 33; it differs from the latter, notably in the occurrence of two instea three nephrostomes and nephrostomal canals. For this reason, the no canal which corresponds to the collecting trunk of Anura, save ion of the latter which intervenes between nephrostomes I. and II.; in discussing the topographical relations of the tubules it will be less to distinguish this remnant of the collecting trunk from the nephrostomal tubule. In this simplest condition of the pronephros, common trunk makes a single loop, the anterior curve of which is ted nearly as far forward as the level of the first nephrostome. In ewhat older pronephridia (Figs. 59, 60) the main bend of the common k occupies a position even in front of the first nephrostome, and a ber of minor folds intervene between the junction of the nephrostomal ls and this most anterior fold. In none of the pronephridia of this e is there any evidence of convolution in the nephrostomal canals.

ne individual of this stage departed from the normal condition, in that ssessed three instead of two nephrostomal canals. This abnormality rred on both sides of the body, and appears to be correlated with a highly developed first nephrostomal tube. It is to be noted that third tubule (Fig. 57) appears as an appendage attached to the posterior loop of the common trunk. This topographical relation ests that it is the most posterior of the three nephrostomal tubules h has been added to those normally present in Amblystoma, and inference is shown to be correct by the relations which the several les bear to the body somites. The question whether the most erior of the three tubules in this case represents the third nephroal tubule of the *Anuran* pronephros can be answered only by a conation of the relations which the several nephrostomes in the two ps bear to the overlying protovertebræ, and will be recurred to in general discussion which follows. I may here anticipate to the extent ating that the first and second tubules of Amblystoma probably espond respectively to the second and third of Rana and Bufo, the rmal third tubule belonging to a yet more posterior metamere.

ne position of the pronephric nephrostomes with reference to the tomes was determined at an early stage by the location of the first meric diverticula which are developed within the pronephric mass; in the present stage these relations have not materially changed. two nephrostomes of the normal pronephros lie beneath the third fourth myotomes respectively. In the case of the pronephridia a supernumerary nephrostome, the first two nephrostomes occur ath myotomes III. and IV. respectively, while the third nephroe is found beneath myotome V.[1]

---

[1] Myotome I. of this enumeration reaches forward to the root of the vagus nerve, is flanked on its outer face by a portion of the ganglion nodosum, exactly as e case of the Anura described.

In this stage the segmental duct in the younger embryos shows so
what different conditions from those found in the older embry
In the case of unhatched embryos possessing the simple proneph
shown in Figure 58, the duct on passing backwards gradually dim
ishes in calibre, and finally loses all trace of a lumen. The fun
ment of the duct is in this region composed of four or five c
in each cross section, which are frequently arranged with some re
larity about the centre as an axis. On proceeding to more poster
regions the fundament of the duct becomes intimately connected w
the mesoderm, and is finally lost in that layer. In Amblysto
the histological characters of the mesoderm and the ectoderm
not sufficiently unlike to allow one to base on them a definite c
clusion respecting the layer which has furnished the material for t
fundament of the duct. In all cases which I have observed, howev
the duct neither unites with the ectoderm nor terminates freely; b
its posterior end invariably is closely applied to the mesoderm, and c
sequently is most probably derived from that layer. In view of the f
that the yolk spherules of the fundament of the duct are of the sa
size as those present in the adjacent mesoderm, I am of opinion th
the duct has undergone no extensive independent growth, but has aris
in situ as a proliferation of the somatopleure.

In the older embryos of this stage, the duct has extended backwa
to the region of the cloaca, and joins the latter near the posterior f
of myotome XX. A distinct post-anal gut is present at this stage.
anterior portion contains an evident lumen, and appears as a direct c
tinuation of the pre-anal portion; its posterior tip is solid, and exte
backward into the tail region for the distance of about one millimet
From the ventral floor of this continuous intestinal tube, a median
verticulum leads backward and downward to the anus. The histologi
characters of this diverticulum differ markedly from those of the rest
the intestine, and by comparison with younger stages it becomes e
dent that the former has resulted from a proctodæal invaginati
Where the intestinal tube is joined by the proctodæum the ventral p
tion, or cloaca, is T-shaped. The lateral arms receive the segmen
ducts, and the ventral stem may be followed to the anus. In Amb
stoma, then, the segmental ducts open into the intestine at the po
where the proctodæal ectoderm and the entoderm pass over into ea
other. It is somewhat doubtful with which of the two germ layers t
wall of the ducts becomes continuous; but it is possible that — in c
trast to the condition obtaining in the Anura studied — the ducts op
upon an ectodermal surface.

In the younger embryos of this stage, the walls of the pronephric bules are all very thick; they gradually diminish in thickness as the nbryo grows older. The lumen, on the other hand, is at first narrow, it afterwards becomes much wider. Its size varies greatly in different rtions of the pronephros. For example, the lumen of the long arm of e common trunk, which forms the direct continuation of the segmental ict, is usually much narrower than the average lumen of the other onephric tubules. The nephrostomal canals near their junction and e adjacent portion of the common trunk usually have a wide lumen. the abnormal pronephros represented in Figure 57, however, the men of the first nephrostomal tubule was very narrow, a circumstance iich, as I have already suggested, may possibly be correlated with the esence of a third nephrostome.

The lining epithelium of the tubes is composed of polygonal cells, iich in the younger embryos have a high columnar form, but become adually thinner as development proceeds. The nuclei when stained th Czokor's cochineal show a coarsely granular or reticulate structure, d are located close to the lumen of the tubule. The protoplasm takes iniform delicate tint, which is masked, however, by the deeply staining lk spherules. These are most abundant near the basal surface of the ll; they decrease in number and in size with the growth of the larva.

In the younger embryos of this stage, the somatopleure is composed somewhat flattened cells, whose superficial dimension is approximately uble the thickness of the cell. The walls of the pronephric tubules these embryos have a thickness of about 37.5 μ, while the parietal ritoneum has an average thickness of only about 15 μ. These two ithelial layers are confluent at the nephrostomes, the wall of the tubule ninishing rapidly in thickness to that of the peritoneum. The phrostomes, as well as many of the pronephric tubules, are slightly gmented on their internal surfaces; but the pigmentation is by no eans so conspicuous as in Rana and Bufo. In the older larvæ of this ge, the peritoneum is much thinner; but since the walls of the tu- les have also diminished in thickness, nearly the same relations are to observed at the nephrostome as in the younger embryos.

As in Rana and Bufo, the pronephric capsule in Amblystoma develops the form of a downgrowth from the somatic layer of the protover- oræ. In Amblystoma the two-layered condition of the capsule and connection with the overlying protovertebræ are maintained in the lest larvæ of this stage. It seems probable, moreover, that the down- owth from the protovertebræ is met by a more or less pronounced upgrowth from the somatopleure immediately ventral to the pronephr The thickness of the capsular sheath gradually diminishes in the cou of the development of the larvæ, but it is in general approximately eq to that of the peritoneum in the same individual. In the older lar moreover, the pronephros, and especially the segmental duct, beco partially covered by a downward extension of the myotome. In su larvæ the anterior limb bud is prominently developed at this stage, a its cells cover in part the posterior ventral portion of the pronephros.

The sinuses within the capsule are bounded by mesenchymatic ce and contain scattered blood corpuscles; they are continuous posterio with the posterior cardinal veins, so that the venous blood in passi forward from the hinder portions of the body bathes the proneph tubules on every side.

The vessel emerging from the anterior end of the pronephros recei a large vessel from the head, and from the point of union the ductus C vieri leads to the sinus venosus. The former vessel is one of the jug lar veins. The distribution of this vein and its probable representat in the adult will be considered in connection with the following stage.

The first trace of the glomus appears in embryos of this stage. consists, as in Rana and Bufo (compare Plate I. Figs. 8, 9, and Plate Fig. 47), of a horizontal fold of splanchnopleure lying close to the dor angle of the body cavity. This fold extends, when fully formed, fr the first nephrostome backwards to the second. The outer layer of t organ consists, as shown by its development, of splanchnic peritoneu which is usually bounded within by a sharp contour. I am of opini that the latter is in reality a thin structureless basement membra The interior mass of the glomus consists of several different elemen In the young stages embryonic blood cells form a prominent constitue Other cells are present, which have an elongated form and are evident connective-tissue elements; and there appear to be still other cells wh are of a less modified character and in which nuclear mitoses occ Many of the latter may well represent young stages in the developme of blood corpuscles, for I have observed mitotic division of blood ce even in certain older larvæ of Stage VI. In addition to the classes cells just mentioned, there are a few large cells whose nature is me quite obscure. These cells measure 60 μ or more in diameter, a contain large yolk spherules, which are closely packed together a make up almost the entire substance of the cell. The histologic characters of these cells ally them most closely with those of the ent derm, and in the youngest stages in which I have been able to ident

n they were closely associated with the yolk entoderm, which lies
tio-ventral to the region of the glomus. It is probable that they
e from the entoderm and migrate into the interior of the splanchno-
ral fold. I have been unable to find in either Rana or Bufo any
similar to these large cells in the glomus of Amblystoma, and I
e at present no suggestion to offer respecting their significance. The
nus, as I have already indicated, is a highly vascular organ, and even
he younger stages it is possible to find vessels which connect it with
aorta. These vessels usually follow the splanchnic layer quite
ely, and appear to lie external to the large cells to which reference
been made.

n the younger larvæ of this stage the body cavity in the pronephric
on has the form of separate chambers, from each of which a single
hrostomal tubule arises; but elsewhere the cavity is wanting on ac-
nt of the contact of the peritoneal surfaces. In the older individuals
expanded over a much larger area, but by the development of the
bud a dorsal portion of the cavity is partially separated from the
as a pronephric chamber.

Stage VI.

Plate VII. Figs. 53, 54. Plate VIII. Figs. 61-65.

he larvæ included in this stage were taken from several different
ngs made in the course of three or four days. They measure about
n. from the anterior end to the tip of the tail. An anterior limb
is plainly visible upon surface view, and the tail is provided with a
nct membranous fin.

he great complication in the structure of the pronephros which is
ined in this stage is accomplished by a continuation of the same pro-
of forming convolutions that has been described for the preceding
e. Indeed, the separation of the two stages is at best quite arbi-
y. Figures 61–65 represent various pronephridia of the present
e. It is to be noticed that the portion of the common trunk of
h the segmental duct is the direct continuation can be traced from
anterior limit of the pronephros backwards without convolution, or
having formed a few insignificant loops. The common trunk from
unction with the nephrostomal tubules to this most anterior bend is
wn into a series of complicated convolutions, which may be so arranged
o present a gradation of considerable regularity (Fig. 62), or may
uite irregular (Fig. 65). In most cases, however, it is to be noticed
the arrangement of the loops is in general favorable for a compact

disposition of the tubes (Fig. 62). The convolution in this stag
no longer confined to the common trunk, the nephrostomal tubules
dergoing slight contortion (Figs. 63–65).

I have determined the positions of the pronephric structures to
somites in these later stages by their relations to the spinal gang
The first and second nephrostomes lie very nearly in the same transv
plane as the first and second spinal ganglia respectively. In the you
est larvæ of this stage the boundaries between the myotomes may
be made out in transverse sections, and the nephrostomes are then fo
to lie beneath myotomes III. and IV. It is probable that in l
stages as well two myotomes occur in front of the first spinal ganglio

The duct after leaving the pronephros pursues a nearly straight co
backwards to the cloaca. In the larvæ of this stage, the post-anal
has atrophied, and the ducts open into the intestinal tract just at
point where it bends downward toward the anus or cloacal apert
The outlets of the two sides of the body are quite widely separa
never opening into an unpaired median depression in the dorsal roo
the cloaca, as is the case in the corresponding stage of Rana. The
lets of the segmental ducts are situated between the eighteenth and
nineteenth spinal ganglion, which would correspond to somite XX
XXI. Their position is, then, the same as in the preceding st
(Compare page 254.)

In the series of embryos included under Stage V., it was shown t
the walls of the pronephric tubules became gradually thinner as the
mal developed. In the pronephridia of the present stage the same
cess has been continued, and the cells are frequently so reduced
thickness that the nucleus appears to be in contact with the basal
well as the superficial, or inner, surface of the cell. Occasionally tu
occur whose walls are so thin that each nucleus causes a protubera
into the lumen of the tube. But wherever the thickness of the epit
lium exceeds the diameter of the nucleus, it is to be noticed that
latter lies close to the inner surface of the tube, whereas the y
spherules are accumulated in the basal portions of the cells. The y
spherules are much less numerous than in the preceding stage.
many cells they are wholly wanting, and in all they now form a mu
less prominent constituent than the cell protoplasm.

The nephrostomes present no new features of interest in this sta
Most of the pronephric tubules contain more or less pigment, which
usually accumulated in irregularly distributed dark patches. In one
two instances I have had a fair degree of success in dissecting out

ronephros of a fresh specimen. In such an isolated pronephros the ourse of the tubes can be followed with tolerable accuracy in conse-uence of the pigmented areas occurring in their walls. The loss of yolk pherules, to which the pronephric tubes have been subjected on reach-g the present stage, is shown in a striking manner by the transparency the gland as contrasted with the snow-white yolk-entoderm.

The histological characters of the duct (Plate VII. Figs. 53, 54) re-mble closely those of the pronephric tubules. Its calibre is greatest in e region immediately posterior to the pronephros (Plate VII. Fig. 54), ecoming less as the duct passes posteriorly (Fig. 53). Throughout its ourse it is accompanied by the posterior cardinal vein (*vn. crd.*). In e older larvæ of this stage, the segmental duct in its passage backwards the cloaca receives a large number of mesonephric tubules, which will described in the sequel.

The pronephros of the present stage is covered on its dorsal surface by e main body of the myotomes. From the outer angle of each myotome, oreover, a distinct fibrillar sheet envelops the entire lateral surface of e gland. This layer is the capsule, whose origin has been discussed in nnection with Stage V. In the present stage, it frequently becomes eply pigmented.

The anterior portion of the pronephros is also overlaid by a stratum smooth muscle fibres, which arises from the dorsal fascia. This mus-lar sheet is continuous in front with a muscle layer which is inserted on the ventral surface of the mandible, and probably represents the pressor maxillæ of the adult.

The pronephros is also covered in part by the shoulder girdle, which this stage is wholly composed of cartilage.

The vascular sinuses enclosed within the capsule are the direct con-uations of the posterior cardinal vein. They also receive — usually out midway between the first and second nephrostomes — a blood-ssel, which may be traced nearly as far back as the cloaca, and which companies in its course the ramus lateralis of the vagus nerve (see g. 53, just median to *n. l.*). I am not aware of any prior mention of vessel having this course, and am unable to state whether this vein s any representative in the adult.

The vessel emerging from the anterior end of the pronephros receives vessel from the head, and the two form the ductus Cuvieri, which pro-eds downward and inward to join the sinus venosus. The anterior anch may be traced forward into the head in the same direction as the iginal trunk ; it accompanies in its course the ramus lateralis vagi.

In consequence of the uncertainty as to what vein of the adult this vessel represents, I shall here digress to describe its distribution at this stage. For purposes of description, I shall follow it from its point of junction with the cardinal vein forward towards its finer branches. Before reaching the ganglion nodosum, it sends a branch dorsalward, which can be traced for a short distance between the lateral wall of the cranium and the ganglion. The main trunk continues forward external to the ganglion, and gives off a branch which passes around the posterior end of the auditory capsule and enters the cranium. The original vessel now passes forward through a narrow channel left between the auditory capsule and the articulating portion of the mandibular cartilage. Near the anterior end of the auditory capsule it divides into two branches, one of which passes dorsal to the eyeball, accompanying in its course the ophthalmic branch of the trigeminal nerve; the other branch passes ventral to the eyeball, and continues into the anterior maxillary region, following the course of the canalis nasalis. The main trunk runs nearly parallel to the aortic root and its prolongation, the carotid artery, the efferent branchial trunks joining the aortic root by passing immediately ventral to the vessel whose course I have been following. The vein evidently corresponds to the one described under Stage V. of Rana (page 233, foot-note), and appears to me to represent in all probability the internal jugular of Gruby ('42) and of Ecker ('64–'82).

The glomus is considerably broader and thicker than in Stage V.; but its longitudinal extent is about the same. In the middle of its course its distal edge reaches across the body cavity and fuses with the somatic peritoneum which covers the pronephros. The structure of the organ appears to be nearly the same as in the preceding stage, but the interior mass is so compact that one can distinguish little more than the nuclei, which present quite uniform characters. Cells which are unquestionably endothelial are frequently evident along the basal surface of the peritoneal layer; they also traverse the interior of the glomus dividing this space into compartments. Pigment is present both in the peritoneal wall and in the interior mass. It has a scattered distribution, appearing in the form of perfectly black patches. The large cells to which allusion was made in Stage V. are present also in this stage. They have about the same size and histological features that formerly characterized them. The pronephric chamber has not changed materially from the condition exhibited in Stage V. The most anterior pronephric tubules are situated immediately lateral to a diverticulum of the body cavity, which in sections through this region appears wholly isolated. On following the eries of sections backward, however, the chamber enlarges greatly, even efore the nephrostomes are reached, and is separated from the ventral ortion of the body cavity only by the lung bud. Between the first and econd nephrostomes, the pronephric chamber is divided into two parts by ie fusion of the distal edge of the glomus with the somatic peritoneum overing the pronephros. Still farther posteriorly, an open communication established, not merely between these two portions of the pronephric iamber, but also between the latter and the general body cavity.

In almost all the larvæ of this stage, the mesonephric tubules have ppeared, and in many individuals they have already opened into the uct. There is always a space intervening between the pronephros and ie mesonephros, in which no tubules are developed. This interval appears to be subject to some variation, but in the majority of cases it omprises four somites.

In the most anterior region of the mesonephros the tubules show traces f a metameric arrangement, but this is wholly lost in more posterior egions. These relations can perhaps be best illustrated by the accompanying table, which shows the positions of the right mesonephric tubules i the larva, whose pronephros is represented in Figure 64. The somites ave been reckoned by reference to the spinal ganglia, but the results are ere expressed in terms of the original metamerism of the myotomes.

Somite III. — Pronephric nephrostome I.
“ IV. — “ “ II.
“ V. — Tubules absent.
“ VI. — “ “
“ VII. — “ “
“ VIII. — “ “
“ IX. — 1 mesonephric tubule.
“ X. — 1 “ “
“ XI. — 1 “ “
“ XII. — 2 “ tubules.
“ XIII. — 3 “ “
“ XIV. — 3 “ “
“ XV. — 4 “ “
“ XVI. — 5 “ “

Each tubule of the mesonephros (Plate VII. Fig. 53) has the ordinary rm, which has induced several authors to call it “sickle-shaped,” and onsists of cells which are wholly devoid of yolk spherules, in which the ucleus occupies almost the entire body of the cell. Along the region hich corresponds to the cutting edge of the sickle, a few loose cells (*fnd.*

glm.') occur, which constitute the earliest fundament of the glomerulu The nephrostomes, however, have not opened at this stage.

In the region between pronephros and mesonephros (Plate VII. Fi 54) certain masses of cells are found on the median side of the duct the same position as that occupied in the posterior region by the mes nephric tubules. These cells do not form a continuous mass, but a interrupted at intervals. The cords of cells thus formed do not, ho ever, appear to correspond in their arrangement to the metamerism the body. It is possible that they represent rudimentary nephridi tubules, but the evidence in favor of this interpretation must be regard as far from satisfactory.

I have been unable to ascertain the precise mode of origin of tl mesonephric tubules, having sought in vain for nuclear mitoses whi should throw light upon this question. There are in younger stag many retroperitoneal (subperitoneal) cells which might be collected ar rearranged so as to produce the tubules; or, again, the fundaments the tubules might be formed by proliferation from the peritoneum. Tl cells of the tubule have evidently undergone very rapid division, as indicated by the complete consumption of the yolk; and this circur stance seems to me to favor the second view. Furthermore, I have foun nuclear mitoses (Fig. 54) in the region immediately in front of the mes nephros which indicate that the cords of cells in this region arise fro the peritoneum. Although I am unable to assert that the mesonephr tubules arise from the peritoneum, I am inclined to regard it as probab that they do. There is no evidence, however, of a definite invaginati of the wall of the body cavity.

This is the oldest stage of Amblystoma which I have examined, ar with it I close the descriptive part of this paper.

III. General Discussion.

Having presented in a purely descriptive manner the facts of develo ment as yielded by my own studies, I shall now endeavor to use the observations as a basis for the criticism of the results of other investig tors, and in closing shall point out certain general conclusions which see to me warranted by such a review.

Recent researches have extended greatly the number of animals which a homologue of the pronephros is known, so that it may now fairly assumed that the organ appears in the ontogeny of all Vertebrat

In view of much recent evidence (Hatschek, '88^b, Rabl, '88, Ayers, '9 hich clearly supports the view that Amphioxus is closely related to raniotes and occupies a position near the base of the Vertebrate phylum, ıe kidneys of this animal are of prime interest in the present connection. 'otwithstanding the extreme importance of the subject, however, the ılation of the excretory system of Amphioxus to other Chordates must ill be regarded as a matter of considerable doubt.

At least seven different views have been advanced respecting the excre-ory organs of this animal. According to the earliest of these views, hich originated with Joh. Müller ('42, p. 101, see also Langerhans, '76, . 322, and Rolph, '76, p. 140), certain modified groups of cells lying in ıe posterior portion of the atrium are claimed to possess an excretory ınction. I presume that no morphologist would endeavor to homol-gize these excretory patches with the kidneys of Vertebrates. The ıme is true of the glandular structures described by Owen ('66, p. 533, ig. 169, *h*), and the epithelial bands of Wilh. Müller ('75, p. 109). 'or can I see in the "pigmented canals," atrio-cœlomic funnels, of ankester ('75, pp. 260, 261, and '89, pp. 394–397) any features which ould definitely link them to Vertebrate nephridia.

The account given by Hatschek ('84) of his discovery of a single ephridium, which he believes to open into the pharyngeal cavity, is too rief to permit one to form a final judgment upon his interpretation. he observation has not been confirmed by any subsequent investigator ıve perhaps Lankester and Willey ('90, p. 459), who do not however gard this organ, which they call the sub-chordal tube, as a nephridium. here is nothing in its structure as described by either author which in y opinion justifies its comparison to a Vertebrate excretory tubule.

The most recent paper on this topic, which is by Weiss ('90), is of ɔnsiderable interest from the physiological researches which it records: ıese show that a large portion of the atrial epithelium, as well as the xcretory patches of Müller, have a well marked excretory function. Of reater morphological value is the description given by Weiss of certain nall tubules in which the excretory function is peculiarly active. These ıbules empty into the atrium at the upper margin of that cavity in the gion of each secondary gill bar. They seem to project into the cœlom, ıt Weiss was unable to detect a continuity between their lumen and ıe cœlom. Since the relations of these tubules to the cœlom are not scertained, I am of opinion that the observations of Weiss do not afford ıtisfactory reasons for regarding them as homologues of either the Ver-ebrate or the Annelidan nephridia. Weiss's account, however, is at ast very suggestive. An important feature is the metamerism of the

tubules; for while the metamerism of the gill bars does not corres
in the adult to that of the myotomes, yet we should not lose sight o
fact that according to Kowalewsky ('67, see his Figs. 36 and 39) su
correspondence exists in the embryo. At such a stage, then, there w
be present a single excretory tubule for each myotome.

In a recent lecture before the Gesellschaft für Morphologie und P
ologie in München, Boveri ('90) has endeavored to show the existen
Amphioxus of homologues of the pronephros, the mesonephros, and
segmental duct. The tubules which Boveri regards as pronephric
probably the same structures as the excretory tubules of Weiss; a
infer that the same have been seen by Spengel ('90, p. 282), though
writer makes no suggestion as to their significance. Both Weiss
Boveri claim to have proved by feeding the animals with carmine that
tubes are actually excretory. According to Boveri, also, they open
the atrium at the upper margin of each secondary gill bar; but t
course is somewhat differently described by the two authors. Bo
maintains that each tube communicates by means of several open
with the dorso-pharyngeal cœlom. As confirmatory of his position
these canals represent the pronephric tubules of Craniota, he desc
the relations they bear to the gill vessels, which he identifies with the
mental vessels described by Paul Mayer ('87, p. 343) in Selachii. Acc
ing to Rückert ('88, pp. 239–242), the glomus of Elasmobranchs con
of a rete mirabile in connection with these segmental vessels. Adja
to the excretory tubules, Boveri finds that the gills display an increa
vascularity, and that anastomoses are formed between the branchial
sels. This condition does not seem to have been noticed by W
Spengel, who made a special study of the gill vessels, describes a lo
tudinal vessel at a corresponding level (longitudinal trunk of the
mentum denticulatum), but does not discuss its significance. It se
to me that Boveri's observations, provided they be confirmed, afford fa
satisfactory evidence of the existence of true nephridia in Amphiox
and, as I shall endeavor to show in the sequel, that these are constru
on a type which may be assumed to represent a primitive condition of
Vertebrate kidney.

The starting point of Boveri's researches was the hypothesis that
atrial cavity and gonadial pouches of Amphioxus correspond to the
mental duct and mesonephros respectively of Craniota. The atten
of Haeckel ('74^{a}, p. 37, and '74^{b}, p. 305) and of Huxley ('76, pp. 2
222) to discover a homologue of the segmental duct in Amphioxus m
in my opinion, be held to have at present merely an historical inter

mains for me to consider whether the theory of Boveri be better
nded.

ne arguments which are adduced in favor of the homology of the
dial pouches and the mesonephros may be reduced to the following
ts of similarity. The gonadial pouches of Amphioxus are metameric
ticula of the dorso-pharyngeal cœlom, in accordance with the estab-
d views of Kowalewsky and Rolph, as confirmed by Boveri, who finds
e adult a continuity of the epithelia belonging to the two tracts; the
nephric tubules likewise are primitively metameric diverticula from
lorsal portion of the body cavity (see Sedgwick, '80^{a}, *et al.*). The
rative cells develop in the walls of the gonadial diverticula; the
occurrence of germinal cells at the proximal ends of the forming
nephric tubes has also been described by Rückert ('88, p. 257) for
hii. Finally, the canal by which the gonadial pouches primitively
nunicated with the cœlom arches over the dorsal angle of the atrial
y in a way that is very similar to that in which the mesonephric
les curve outward to join the duct. The only reason — save those
require the prior assumption that the gonadia represent mesonephric
les — which I can see for identifying the atrium with the segmental
is the fact that nephridial (pronephric?) tubes open into it. This
ment seems to me of very little weight. Boveri himself believes that
ronephros primitively opened directly to the exterior. Unless other
nce can be adduced, I see no adequate reason for regarding the
ation of the atrial cavity as a step in the development of the seg-
al duct. On the other hand, that interpretation seems to me quite
sed to all that is known of the development of the segmental duct.
have shown in the preceding pages, there can be no doubt that,
mphibia at least, the duct develops solely from the mesoderm.
rding to the opposed view — the ectodermal origin of the duct — the
lopment always proceeds from a *pair* of narrow rod-like thickenings
toderm, one on each side of the body, which are very different from
npaired ventral groove from which, according to the most recent
unt (Lankester and Willey, '90) the atrium develops. If, now, we
the homology of the atrium with the segmental duct, the outward
ng of the gonadia becomes a most insignificant topographical resem-
e. It seems to me that it would be manifestly unfair to base so
aching a homology on the remaining points of resemblance, viz. the
occurrence of germinal cells in the mesonephric tubules, and the
mstance that the gonadia are metameric diverticula of the dorso-
yngeal cœlom.

Turning now to Craniota, the pronephros in Amniota and Sela is a wholly degenerate structure ; in many Anamnia, however, it se for a longer or shorter time as a functional excretory organ.

The pronephros of Dipnoi alone is wholly unknown. Beard (p. 157) speaks of the transformation of a part of the pronephros into Müllerian duct as "a well known fact"; but the only authority he c in this connection (Parker, '89) does not make such a statement, have I succeeded in finding anywhere in the literature any account of pronephros of Dipnoi. Unless Beard has personal observations on matter, I believe that in Dipnoi absolutely nothing is known of pronephros or its transformation, save such inferences as may be dr from the adult anatomy. I shall therefore merely repeat the statem of Ayers ('85, p. 506), that the development probably proceeds a Amphibia, since the adult urogenital system in this group presents closest analogy with that of the Dipnoi.

The excretory system of Cyclostomes is similar to that of Amphi In Petromyzon a pronephros develops in the Ammocœtes larva, aborts in the adult. The number of nephrostomes and of tubule small (4, according to Wilh. Müller; 4 to 5, Shipley; 3, Kupf according to Semon, an inner and an outer row of nephrostomes to be distinguished); and they communicate with an anterior expan portion of the body cavity. According to Fürbringer ('78^a, p. 42), pronephros extends over about four somites. Opposite the nepl stomes, a vascular organ projects from the root of the mesentery i the body cavity. This is the so-called glomerulus; as figured by S ('81, Taf. IX. Fig. 24), it strikingly resembles the glomus of A phibia. According to Scott, the pronephric tubules develop seconda as outgrowths from the segmental duct. On the other hand, Shipley confirmed the statements of Müller and Fürbringer, according to wh the nephrostomes and tubules are formed by the incomplete clos of a longitudinal groove of somatopleure. Finally, Kupffer maint that the tubules arise as *three separate evaginations of the somatople* a result which is in harmony with my own observations on Amphibia

In Myxine nothing is known of the early development ; but in l stages an organ has been made known by the studies of Wilh. Mü

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[1] In Goette's ('88, p. 163) preliminary account of the development of Petromy he states that a pronephros develops in the *same* manner as in Amphibia. T would indeed be a conclusion acceptable to me, but until the accounts are mor one in regard to the latter group the statement is somewhat vague. I await v interest the publication of that portion of Goette's final paper which relates to excretory system.

) and of Fürbringer ('78^{a}, pp. 38, 39), which plainly represents the
phibian pronephros. Whether it ever persists in the adult is still a
ter of doubt (see Weldon, '84) ; but in young individuals, at least,
segmental duct (ureter) is prolonged anteriorly to the heart region.
e it gives off numerous coiled tubes, which branch and open by funnel-
ped nephrostomes into the pericardial cavity. On its dorsal side,
duct gives off a few tubules which terminate in glomeruli resembling
se of the mesonephros. This condition and the large number of
ules constitute the main points of difference between the Amphibian
nephros and that of Myxine.

he pronephros of Teleosts and Ganoids appears to me to be reduci-
to a single type of structure, which can be easily derived from the
dition present in Amphibia and Cyclostomes (and Dipnoi ?). The
alled head-kidney of Teleosts described by Hyrtl ('51, p. 29) is prob-
derived from the embryonic pronephros, though mesonephric ele-
ts may also be found in the adult head-kidney (see Emery, '82,
6).

ccording to Rosenberg ('67, pp. 42 *et seq.*) and Oellacher ('73, pp. 97–
), the excretory organs arise as a pair of grooves of the somato-
ire directly beneath the protovertebræ. A process of constriction,
ch proceeds from a middle region forwards and backwards, leads to
conversion of each groove into a tube, the segmental duct. The
erior portion becomes wholly cut off from the body cavity, and is
wn into numerous coils. The tip becomes considerably swollen, and
nvaginated by an outgrowth from the aorta forming a single glomer-
s on each side.

oette's ('75, pp. 826, 827) account of the development of the pro-
hric glomerulus in Teleosts is somewhat different, and affords a better
s for homologizing the pronephros of Teleosts with that of Amphibia.
tte maintains that the somatopleural groove is imperfectly closed
front, leaving a single nephrostome, opposite which a glomerulus
mus) is developed. Subsequently, the pronephric chamber becomes
rated from the rest of the body cavity, and comes to resemble a
pighian capsule with its contained glomerulus. While Fürbringer
^{a}) confirms Goette's view, Hoffmann ('86, p. 621 *et seq.*) has quite re-
tly reasserted that this Malpighian capsule is the blind infolded end
he segmental duct, and the homology with the Amphibian glomus
pronephric chamber, which appears to me probable, he denies.
fmann's position does not seem to me tenable in the light of com-
ative studies. Even though it should be shown that the ducts

have absolutely no connection with the body cavity at the time wh the glomerulus is formed, I could nevertheless defend my position the assumption that the blind anterior end of the duct is a compou structure, representing both nephrostomal canal and pronephric cha ber. It seems to me that, were it necessary to make this assumpti an extensive comparative study would justify such an interpretation.

The pronephros of Teleosts was long supposed to remain functio in the adult; but recent investigations seem to favor the conclusion t it never persists in fully mature individuals, with the possible excepti of a few degenerate animals like Fierasfer (cf. Balfour, 81^b^, '82; Grosgl '85 and '86; Emery, '80, '81, and '85; Calderwood, '91).

The account given by Balfour and Parker ('82, pp. 415–424) of t development of the pronephros in Lepidosteus is in very close agr ment with the development in Teleosts as described by Goette and Fürbringer. The only conspicuous point of difference is, that, while Teleosts the pronephric chamber becomes wholly detached from the bo cavity, in Lepidosteus a remnant of the original communication probal persists as a so-called peritoneal tubule. As among Teleosts, the p nephros atrophies in adult Lepidostei.

Beard's ('89, pp. 114, 115) account of the early development diff greatly from that just given. According to this author, the proneph is formed as a solid proliferation from the intermediate cell la (Balfour) in the region from the 4th to the 8th or 9th somite inclusi Externally, the proliferation fuses with the ectoderm. As a rule, th are formed three pairs of pronephric nephrostomes, of which the m posterior pair abort. The pronephric chamber is formed by the narro ing of the ciliated opening and the widening of the part opposite t glomerulus. Since Beard does not describe the development of t glomerulus, the account seems to me decidedly vague; but I belie I am right in accrediting to the author the view held by Hoffmann Teleosts, that the glomerulus is not developed in the body cavity. I understand him, it is developed in the course of the proneph tubes.

All the studies on Ganoids thus far enumerated have been made up Lepidosteus. In Acipenser, Salensky ('78, '80) maintains, in opposition Kowalewsky, Owsjannikoff and Wagner ('70), that the excretory orga first appear as a differentiation in the form of a solid cord of cells. The is at that stage no trace of the cœlom, nor of a division into protovertebr and lateral plate. Indeed, this cord of cells first marks the region whe the latter separation will later occur. In its further development t of cells acquires a lumen, either by a rearrangement of the cells, or estruction of the axial ones. Anteriorly the structure now opens the body cavity. The anterior portion elongates and becomes more nore convoluted up to the time of "post-embryonic" development. site each of the peritoneal funnels are formed glomeruli [glomi] as esses from the radix mesenterii. They are covered by a pigmented of peritoneum. Salensky does not seem to me to have been very upon the earliest development, which was studied mainly by surface , and I am of opinion that these stages would show very different itions if more recent technical methods were employed. The most esting feature of the development, as described by Salensky, is the rrence of a glomus in the position which is typical for Amphibia and omyzon.

e excretory system has probably been studied more carefully in hii than in any other group. The independent researches of Bal- ('75 and '78) and Semper ('74 and '75) are in substantial accord, have formed the basis for all subsequent investigations. For our ose, the most prominent feature of the development as described hese authors is the absence of any structure which demonstrably sents the pronephros. According to Balfour, the first trace of the tory system appears as a solid knob springing from the "interme- cell mass" near the level of the hind end of the heart. From this ior proliferation a solid cord of cells grows backward between ecto- and mesoderm. The posterior portion is the fundament of the ental duct; the anterior knob persists in adult females as the m abdominale of the oviduct. According to Balfour, this solid represents a rudimentary pronephros.

ry recently the early development of the excretory organs has been d in a new light by the researches of Rückert ('88) and van Wijhe . According to Rückert, the development begins with the forma- of a pronephros as an outgrowth towards the ectoderm from the al portions of several *protovertebræ*, extending from the third or h trunk somite backwards for a distance of four to six somites. thickening extends ventrally in each somite to the region where the ented mesoderm passes into the unsegmented lateral plates. The feration, in the formation of which the somatic layer is alone con- d, shows on careful study a metameric character. From the pos- r end of each protovertebra a narrow canal can be traced outwards backwards, where it unites with a similar canal emerging from the following somite. The pronephric mass fuses for a time with the

ectoderm and probably receives a contribution of cells from that la
The duct grows backwards as far as the cloaca at the expense of
ectoderm. Having reached this stage of development, the proneph
rapidly degenerates. This process takes place in a slightly different
in the anterior and posterior regions. A variable number of the m
anterior evaginations flatten out into a simple longitudinal groove of
itoneum, the ostium abdominale; the remaining ones become closed
detached from the peritoneum; thus there remains a longitudinal ca
communicating with the body cavity by the slit-like ostium. In in
preting the structure as a rudimentary pronephros, it is important
note the discovery by Rückert (pp. 239–242) of a structure which he
gards as a pronephric glomerulus, or glomus. This structure is develo
in connection with segmental blood-vessels which pass from the aorta
the right subintestinal vein, and which have been described by
Mayer ('87, p. 343). In Torpedo the vessels are present on the right
in the same number as the segments of the pronephros, and as they
ventrally between the entoderm and the splanchnopleure it is to be noti
in regard to the middle vessels at least, that they send out buds, wh
form projections from the median peritoneal wall opposite the proneph
tubules.

It will be at once seen that the development of the pronephros as
scribed by Rückert is in striking agreement with the account I h
given of the early stages in the development of the Amphibian
nephros, and I have no hesitation in homologizing the two organs.
earliest stage which has been observed in both groups is that whic
have termed the pronephric thickening. This is followed in both by
stage of canalization; but the Selachian pronephros never goes bey
an early condition of the pronephric pouch, in which, however, the ho
logues of the nephrostomal tubules and the collecting trunk app
The points of difference between the account I have given and
given by Rückert for corresponding stages of the Selachian proneph
seem to me, with a single exception, to be either unreal or insignific
The exception to which I refer pertains to the participation of the e
derm in the formation of the pronephric thickening. This conditio
am confident does not occur in Amphibia. Moreover, the evidence u
which Rückert bases his statement seems to me far from conclusive,
has his observation been confirmed by any subsequent investiga
Rückert described the pronephric thickening as a product of the pr
vertebræ. I cannot admit that this is true for Amphibia; but I bel
that our differences of opinion are really due to the fact that we use

erent criteria for determining the boundaries of the protovertebræ. 'here can be no doubt that the earlier pronephric thickening is made p of metameric constituents; but I should be unwilling to regard ll segmented mesoderm as belonging to the protovertebræ. On the ontrary, I am of opinion that the ventral extent of the protovertebræ for the first time defined when the longitudinal constriction appears 'hich divides the primitive cœlom into protovertebral cavity and pleuroeritoneal or (secondary) body cavity. When such a definite line of emarcation has been established, the remnant of the pronephros in elachii, as well as the functional pronephros in Amphibia, remains conected with the latter space. The remaining points of difference relate the number of tubules involved, — which, as we have seen, varies ven within the class of Amphibia, — and to their position with referace to the somites. The latter feature seems to me to be at once ifficult to determine and of minor importance.

Before the conclusion of this paper I shall endeavor to indicate how e glomus of Amphibia may possibly have been derived from the pe of structure which is described by Rückert for Selachians and by overi ('90) for Amphioxus.

The results gained by van Wijhe ('89) do not seem to me to differ om those of Rückert in many respects which are of importance for a omparative study. The great divergence of their descriptions in the se of many details seems to me to be occasioned mainly by the peculiar onception which Rückert holds of the relations between the protoverbral and the lateral mesoderm. For these details and for the hotly ontested questions of priority, I must refer to the original papers (van 'ijhe, '86, '87, '88^a, '88^b, '89, Rückert, '88, '89), and consider here those atures only which merit special attention because of their bearing on e general questions of homology. Van Wijhe denies positively the rticipation of the ectoderm in the formation of the pronephric thickeng; and he claims that the ostium abdominale is formed from the proephros by the fusion of the nephrostomes. Finally, structures which are pposed by him (pp. 480–482) to represent the pronephric glomeruli Rückert are described as occurring on both sides of the body, not, affirmed by Rückert, on the right side alone, and van Wijhe inclines the view that they are actually equivalent to the glomi of Amphibia. he body described by van Wijhe consists of a vascular rod, which passes liquely from the dorsal to the ventral lip of the pronephric pouch, and presents the last trace of the partition between two peritoneal opengs, which have not yet fused. Rückert's description is not entirely clear, and also suffers from misleading typographical and grammati errors; but it is certain that the structure he describes lies within splanchnic peritoneum, and is not to be confounded, as was done by Wijhe, with the partition between two pronephric tubes. Rückert s ('88, p. 239), "Es [ein Paul Mayer'sches Quergefäss] zieht dicht an medialen Grenze der Vornierenanlage vorbei und gelangt, indem es Leibeshöhle durchbricht, d. h. ihre Wandung vor sich herstülpt, an Aussenfläche des Darmes, wo es zwischen Ectoderm [soll wohl Entode heissen] und Splanchnopleura gelegen, mit der rechten Subintestinalv confluirt." I cannot admit that the structure described by van Wi is the homologue of the Amphibian glomus, nor do I believe that corresponds to the structure observed by Rückert.

The mode of development of the excretory system is much alike in three groups of Amniotes. It seems, however, best in the present stance to deal with the Reptiles separately from Birds and Mamm The most important of the works on the Reptilian excretory system perhaps the monograph of Braun ('77), which, however, is of little vice in elucidating the earliest stages. Weldon ('83) first gave a sa factory account of the early development. According to this author, first trace of the excretory system in Lacerta is found in the region the intermediate cell mass, and consists of a series of vesicles (Segm talbläschen of Braun), which have a strictly metameric arrangeme Throughout a region of five protovertebræ (from the 8th to the 12 there appears on the external wall of these segmental vesicles a rod cells at first composed of discontinuous parts. This rod is the fundam of the segmental duct; in the region between two successive proto tebræ, it is budded off from the unmodified "middle plate" (Waldey or intermediate cell mass. Behind the twelfth protovertebra, the d grows backward, free from adjacent tissue. The rod of cells soon quires a lumen, continuous anteriorly with the cavities of the segme vesicles.

The observations of Mihalkovics ('85) upon Lacerta agilis differ fi those of Weldon mainly in two particulars. In the first place, accord to Mihalkovics (pp. 42, 43), the most anterior three or four pairs of mental vesicles at the time of their origin communicate both with body cavity and with the protovertebral cavity. In other words, t are formed as expansions of what I have termed the communicat canal, or Mittelplattenspalten of the German authors. Some som in the series, however, may be without vesicles. Secondly, Mihal vics (p. 48) maintains that the segmental duct buds off from the mid te as a *continuous* cord of cells at a time when only the first trace the segmental vesicles has appeared. Before the (3 or 4) anterior gmental vesicles have entirely lost their connection with the body vity, they communicate distally with the lumen of the segmental duct, d may therefore be regarded as typical nephrostomal canals. This ndition is never encountered in the posterior vesicles, which develop lependently of the cœlom in the solid Wolffian blastema, or middle te. In consequence of this difference in the mode of development the anterior and posterior portions, Mihalkovics is of opinion that the t three or four segmental vesicles represent a rudimentary pronephros.

According to Strahl ('86), the segmental vesicles are budded off from ventral portions of the protovertebræ, and gain secondarily a con- tion with the body cavity; the duct does not appear until the vesicles evident.

Ostroumoff ('88^b, p. 81) confirms for Phrynocephalus the observations Mihalkovics regarding the anterior segmental vesicles, although he is ble to ascertain the precise number that communicate with the body ity. He also interprets these anterior vesicles as a pronephros. The t, however, first appears in disjointed fragments lying between cessive vesicles.

According to Hoffmann ('89), there develops in Reptiles a pronephros ilar to that described by Rückert ('88) for Selachii. It appears as a ies of evaginations of the somatopleure. These are formed in the re- n where the protovertebræ pass over into the lateral plates. The organ ends over a variable number of somites (6–7 in Lacerta and 5–6 in Tro- onotus). As protovertebræ separate from the lateral plate, the pro- hric evaginations remain in connection with the former, except in the e of the first outgrowth (L. agilis, in L. muralis the first two), which ns for a time a single pronephric ostium. The most posterior out- wth extends backwards, and forms the fundament of the segmental t. The fate of the several evaginations is different. The most ante- and possibly the next following outgrowth abort at an early stage; remaining evaginations become detached from the protovertebræ and with one another, thus forming a tube closed in front, but continu- posteriorly with the segmental duct. Hoffmann identifies these ginations with the segmental vesicles of Mihalkovics and Weldon, asserts that these authors mistook for a separate fundament of the mental duct a blind backward prolongation of the evagination belong- to the immediately preceding somite. These backward processes are cribed by Rückert for Selachii. Ostroumoff's ('88^b, pp. 78, 79) statement, apparently unknown to Hoffmann, that the duct first appea short fragments, each of which lies posterior to a segmental ves could be readily brought into accord with these observations.

In regard to the correctness of Hoffmann's conclusions that these ev nations represent a pronephros, I am of opinion that there is consider room for doubt. The organ described by Hoffmann differs in two portant respects from that of Selachii, and from the young stages of Amphibian pronephros as presented in the first part of this paper. the latter groups, while the metameric evaginations are yet contin with the cœlom, they have also fused distally to form a longitud canal (collecting trunk); this condition I wholly miss in Hoffma account, according to which all the evaginations remain distinct f each other till they have entirely separated from the cœlom, and the more posterior outgrowths ever fuse together. Secondly, no st ture comparable to the Amphibian glomus is described. The la objection would apply equally to the account given by Mihalkov None of the previous investigators were more successful in fin glomeruli of the pronephric type.

In regard to the former feature, however, the account of Mihalko is more satisfactory, since the most anterior three pairs of vesicles st in precisely this relation to the body cavity and to the collecting tr (segmental duct). In reviewing Mihalkovics's interpretation, Hoffm says ('89, p. 272), since "die Vorniere als eine Ausstülpung, die Urn nicht als solche entsteht, kommt es mir höchst wahrscheinlich vor, die Vermuthung von Mihalkovics, nach welcher die proximalen Urnie kanälchen der Eidechsen der Vorniere der Amphibien entsprechen, andere Deutung zulasse." I judge from this passage that Hoffman inclined to regard as mesonephric tubules the anterior three or four mental vesicles described by Mihalkovics. I am quite unable to monize this view with Hoffmann's prior identification ('89, pp. 267, 2 of the pronephric evaginations described by him with the segme vesicles of Mihalkovics and Weldon. The mode in which the m nephric tubules develop in Lacerta is asserted to be very similar to described by Rückert and van Wijhe for Selachii. If I properly un stand Hoffmann's description, the space lettered *c.* in Tafel XVII. Fig and 4, is the lumen of a mesonephric tubule. From these figures evident that the mesonephric tubule develops from a portion of m derm ventral to the pronephros; but according to both Rückert and

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[1] Figures 18 and 19, referred to by Wiedersheim ('90^b, p. 413) in this connect do not relate to Reptiles at all. They represent sections of Duck embryos.

jhe, the mesoderm which produces the mesonephric tubules in Selachii
ongs to a region dorsal to that which gave rise to the pronephros
the diagrams appended to van Wijhe, '89, Taf. XXXII.).
n view of the difficulties to which I have alluded, it seems to me that
ffmann's position cannot be regarded as satisfactory. Furthermore, if
ffmann's observations[1] on the origin of the posterior mesonephric
ules be accurate, the contrast which Mihalkovics endeavored to es-
lish between the anterior and posterior tubules does not exist. If,
lly, these anterior three or four pairs of tubules develop in their
rse typical Malpighian capsules remote from the peritoneum, — Mihal-
ics is not clear on this point, — I can see no reason for regarding them
ronephric. I am therefore of opinion that there is at present no
dence which *proves* a pronephros to exist either in Lacertilia or in
idia.
t remains for me to consider two recent papers by Wiedersheim
^{a}, '90^b), which describe a very interesting condition of the excretory
tem in Crocodilia and Chelonia. The anterior portion of the em-
onic excretory organs in these groups consists of a number of
ules which take their origin in ciliated nephrostomes, and, after un-
going contortion, join a longitudinal canal continuous with the seg-
ntal duct. From the root of the mesentery a large glomus protrudes
the body cavity. It lies in a distinct fold of the peritoneum, and
sists of a mass of highly vascular tissue receiving distinct vessels
n the aorta. It extends continuously opposite a number of nephro-
nes, and is evidently equivalent to the Amphibian glomus. In some-
t more posterior regions the conditions are essentially the same;
the nephrostomes and the glomus having approached each other,
y are cut off from the main portion of the body cavity by a longitu-
l fold of peritoneum. In this manner, there is formed a pronephric
mber comparable to that of Amphibia. In yet more posterior regions,
pronephric chamber with its contained glomus breaks up into a series
apsules containing glomeruli, each of which then appears to form the
d termination of a tubule. This is the region of the mesonephros with
ical Malpighian capsules. In the subsequent development of the em-
o, the anterior portion of this excretory system early atrophies, and
hinder part alone constitutes the well known Wolffian body, or
onephros. In my opinion, the account given by Wiedersheim affords
tisfactory basis for the view that the most anterior portion of this
retory system is truly pronephric. It seems, however, quite impos-

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[1] Similar observations are recorded by Orr ('87, pp. 325–327).

sible to draw a rigid line between pronephros and mesonephros. Inde such is a part of the conclusion which I think we shall finally be able draw from the entire review.

The numerous accounts which have been recently given of the p nephros in the higher Amniota may be conveniently treated under th heads : —

(1.) According to Balfour and Sedgwick ('78, '79), the Müllerian d in the Chick first appears in a region somewhat behind the front end the Wolffian duct as three slender invaginations of the peritoneum wh covers the Wolffian body. These invaginations later fuse at their dis extremities, and the most posterior involution grows backwards in c nection with the Müllerian duct. There is thus formed a longitudi canal with three peritoneal funnels, the whole structure being compara to the pronephros of Amphibia. Slightly in front of the nephroston there is attached to the radix mesenterii a vascular body which resemb the Amphibian glomus. It receives blood-vessels from the aorta, a projects into the body cavity enclosed in a distinct sac of peritoneu Gasser ('74, pp. 58, 59) had previously observed somewhat similar con tions in the anterior end of the Müllerian duct; and, by renewed inv tigation, Gasser and Siemerling were able to confirm the occasion occurrence of the phenomenon, though a single invagination appea to be the rule. Multiple invaginations have also been mentioned Kollmann ('82^{b}, p. 20), Siemerling ('82, p. 29), Janošik ('85, p. 43), a Mihalkovics ('85, p. 295); but Braun ('79) and Renson ('83, p. 37) w unable to find any evidence of such a condition. Braun also oppo Balfour and Sedgwick in their view respecting the nature of the vascu body, and Sedgwick ('80^{b}) later came to the conclusion that this str ture was really a series of greatly modified mesonephric glomer This interpretation was adopted by Balfour ('81^{a}, p. 590).

(2.) The second view is set forth in the recent account of Felix ('9 who describes in a chick embryo with eight protovertebræ a series outgrowths, which, emerging from the lower hinder portions of protov tebræ IV.–VIII., extend backward and outward toward the ectoder The latter layer occasionally presents local thickenings in this region, a in some cases a connection between the mesodermal outgrowths and t ectodermal thickenings can be observed. In older embryos no trace the structures can be found. As was the case with the evaginatio found by Hoffmann ('89) in Reptiles, no fusion of their distal extremit is recorded. This condition makes them at once unlike the Selachi pronephros described by Rückert, and the early stages of the Amphibi

onephros as detailed in the preceding pages. Moreover, Felix pro-
ces no evidence to show that they stand in any genetic relation what-
er to the Wolffian duct, or to the pronephric structures described by
ner authors. In the present state of knowledge his interpretation
ems to me untenable.

(3.) The remaining views all have the common feature that they regard
rtain rudimentary canals in connection with the anterior end of the
olffian duct as pronephric. The views are somewhat divergent, but I
ve been able to compile from them a general statement which will in
neasure explain their conflicts. In bringing the observations of each
thor under this general scheme, I shall frequently be driven to regard
results as incomplete, but I shall as far as possible avoid questioning
statements from an *a priori* standpoint.

In general three regions of the embryonic excretory organ may be
tinguished: the pronephros, an intermediate region, and the meso-
phros. For criteria of these regions, I shall use in the main glomeru-
structures: those of the pronephros are glomi wholly external to the
bules; those of the intermediate region are transitional glomeruli,
ich develop in peritoneal canals, but project through the nephrostomes
o the body cavity; those of the mesonephros are typical glomeruli,
ich have only a mediate connection with the body cavity through the
bule.

It now remains to consider the results of the observers whom I have
ced in my third group. The work of Gasser and Siemerling ('78, '79),
bsequently carried on by Siemerling ('82), relates to Birds alone. These
thors recognize two distinct portions of the Wolffian duct: a portion
ng in front of the fifth somite, and a posterior portion. The former
ows many irregularities, is broken up into discontinuous fragments,
d early atrophies; the latter develops more slowly, but more regularly,
d persists as the duct of the Wolffian body. The first indications of
bules consist of the so-called primary cords, which are continuous with
cœlomic epithelium by means of funnel-shaped ostia, while they are
tally in contact with the duct. Gasser and Siemerling maintain that
ey belong to the most anterior part of the mesonephros, a portion which
ly atrophies. They are quite similar to the S-shaped canals of Kölli-
('79). In front of the region of the "primary cords" similar evagi-
tions occur, but these never reach the duct. A typical glomus, which
y be single or may be divided into parts, projects from the radix
senterii opposite the openings of these evaginations. In embryos
this stage the space between the most anterior Wolffian tubule and

the pronephric structures is traversed by a series of glomeruli which semble most closely those of the mesonephros. Siemerling calls th transitional glomeruli. The pronephros of our scheme would be re sented in this account by the region in front of the fifth protoverteb the intermediate region would correspond to the space occupied by transitional glomeruli, and also, as I believe, to that previously occup by the primary cords; the mesonephros would form the rest of organ.

According to Sedgwick's ('81) account of the development in chick, the Wolffian duct, in separating from the proliferation in wh it arises (region between the 7th and 11th protovertebræ), rema connected with the peritoneal epithelium by short cords of cells. tween the 8th and 15th protovertebræ, the duct, as it grows freely ba wards, comes secondarily into contact with such a cord of cells in e somite. Behind the 15th somite, the fundaments of the tubules (int mediate cell mass) do not join the duct until their differentiation somewhat advanced. The cords of cells in the region between the and 11th protovertebræ acquire lumens which may be continued e into the duct; but both cords and duct soon entirely disappear. though no glomus is described, this region probably represents pronephros. Between the 12th and 15th protovertebræ typical nep stomal funnels are formed, in which transitional glomeruli develop. T portion of the organ would then correspond to the intermediate regio the general scheme; behind this region comes the typical mesoneph Sedgwick regarded the first mentioned region as pronephric; but hoped to be able to harmonize such a view with the position (*cf.* page 2 formerly taken by himself and Balfour (Balfour and Sedgwick, '79).[1]

In the foregoing description I have assumed that the most ante portion of the Wolffian duct and the accompanying transverse ca observed by Sedgwick corresponded to the pronephric region as scribed by Siemerling. This interpretation seems to me in all proba ity correct; yet it should be recalled that the pronephros described Siemerling lies in front of the 5th somite, and is anterior to the reg in which the early proliferation to form the duct took place; wher

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[1] Mihalkovics's statement, that Sedgwick abandoned his former view, is in rect, as will be seen by referring to the closing paragraph of his article (Sedgw '81, p. 468).

In the second edition of Foster and Balfour's ('83, p. 218) Elements of Em ology, revised by Sedgwick and Heape, the anterior end of the Müllerian duct is only homologue of the Amphibian pronephros suggested.

pronephros, according to Sedgwick, lies between the 7th and 11th
overtebræ and arises in the same region in which the duct first
ears.

ockwood ('87, pp. 657–663) describes three regions in the embryonic
etory organ of the Rabbit. In the most anterior region (pronephros),
duct consists of isolated fragments, which are connected with the body
ty by 2–3 nephrostomes. Then follows a region of typical nephrosto-
canals with glomeruli, and finally typical blind mesonephric tubules.
ibly the last two regions belong to the mesonephros; but in none
ne accounts of Mammalian development have I been able to recog-
with certainty the intermediate region.

ccording to Renson ('83, p. 29), glomeruli develop in the Chick in
region of the pronephros, which is otherwise described in agreement
Sedgwick's account. The pronephric tubules atrophy with the
ption of their nephrostomes, and in the hollow of each funnel there
ears a glomerulus which soon comes to project freely into the body
ty. In a region directly posterior to that in which the free glomeruli
r, there are found the so-called mixed glomeruli, which are situated
ne base of an infundibular depression, and are partially covered by
ld of peritoneum. This, as well as the more anterior portion of the
em, Renson regards as belonging to the pronephros. He also de-
es in the Rabbit a series of peritoneal involutions in connection
a discontinuous duct. In this region he likewise observed a vascu-
tructure, which he regarded as a very rudimentary external glomer-
. A similar observation has been recorded for human embryos by
wood ('87, pp. 662, 663), and for Arvicola by Spoof ('83, p. 86, foot-
). It is difficult to arrive at a satisfactory estimate of Renson's posi-
. There would be no difficulty in classing him with Sedgwick, were it
for the circumstance that he describes for the pronephric region (6 or
to 11 or 12th somites) glomerular structures which, according to his
comparison, develop in the same way as the transitional glomeruli
rved by Sedgwick in the "intermediate" region only (11th to 14th
te). If, however, it should prove to be true that only the "mixed"
eruli develop in this way, the conflict would at once be removed, and
son's account would show the three primary regions in their typical
lition.

ccording to Mihalkovics the most anterior two or three tubules (4–7
ites) in the Chick and Duck are derivatives of the communicating
ls, and gain a connection with the duct while yet opening into the
cavity by a distinct ostium. The posterior canals, on the contrary,

are all differentiated from the solid "Wolffian blastema," and never l any connection with the body cavity. Posterior to the last pronep canal, 5–6 free glomeruli are to be found. The anterior canals i much earlier than the posterior, indeed they wholly abort before mesonephros attains its final development; and they together with free glomeruli are, in his opinion, to be regarded as equivalen the pronephros and glomus of Amphibia. Mihalkovics also ment the occurrence of transitional glomeruli; these are typical glom which lie near the peritoneal covering of the Wolffian body. It se to me probable that these glomeruli really belong to the mesonep and that at least a portion of the "external glomeruli" belong in re to the class which I have designated transitional glomeruli. This i pretation would not merely be in agreement with the described pos of the glomeruli with reference to the somites, but it would also ac well with the figures Mihalkovics gives of the two sets of glome Thus, in his representation of a transitional glomerulus (Taf. 1. Fig *g. m.*), there is little reason to regard the structure as in any way diffe from a mesonephric Malpighian body. I may here further remark, nearly all other modern investigators agree in deriving a part, if not of the mesonephros from a layer of cells which primitively bounded cœlom, rather than from a strictly indifferent blastema. In this li the validity of the principal contrast Mihalkovics sought to establish tween the pronephros and mesonephros becomes at least very uncert

The account of Janošik ('85) affords the best basis for the ger scheme I have proposed. The most anterior region, or pronepl develops somewhat *later* [!] than the first tubules of the mesonep (primary cords ?). The duct in the region of the pronephros is br up into fragments, which receive rudimentary peritoneal canals. T typical glomi are developed on the radix mesenterii. In the next fol ing region (intermediate), from two to five peritoneal canals communi with the Wolffian duct. Near the nephrostomal ends of these ca transitional glomeruli develop. Both the pronephros and the interm ate region rapidly atrophy. The remaining portion of the embry excretory organ is the true mesonephros. The mesonephric tubules either developed as separate buds from the peritoneum, or are diffe tiated from a blastema which is directly derived from the peritone Janošik was able to confirm Renson's discovery of rudimentary nephric tubules in the Rabbit, but was unable to find in this form trace of external glomeruli. Later, however, he ('87, p. 582) describe a young human embryo, 3 mm. in length, a peculiar projection into

cavity. The structure resembled the external glomerulus of Birds,
e was inclined to interpret it as such in this case.
the preceding pages I have endeavored to present a comprehensive
né of the development of the pronephros as described in groups of
brates other than Amphibia. In this review it has been shown
an equivalent of the Amphibian pronephros has been claimed to
in all Craniota; and that a mode of development similar to that
ibed in the early part of the present paper has been found in
hii by Rückert ('88) and van Wijhe ('89), in Petromyzon by
fer ('88), and in Lepidosteus by Beard ('89). The Reptilian
phros as described by Hoffmann ('89), and that of the Chick
ding to the account of Felix ('90), do not seem to me to be in per-
ccord with this mode of development.

now remains for me to compare the results of my studies, as detailed
e descriptive part of the present paper, with those which have been
led by other writers on the development of the Amphibian proneph-
According to the account which at present receives most general
tance, the pronephros first appears as an outfolding of the somato-
e in the form of a longitudinal groove. The anterior end of this
e is destined to become the pronephros; the remaining portion is
ricted off to form the segmental duct. Since the process of con-
ion advances from before backwards, stages may be found in which
npleted tube is continuous posteriorly with a mere groove of the
topleure. In the anterior region, the groove remains in communica-
vith the body cavity, and grows down towards the ventral surface
e embryo in the form of a broad pocket. The slit-like peritoneal
ng of this pouch closes throughout the greater part of its length,
ng, however, two or three regions of incomplete closure, the funda-
s of the nephrostomes. The nephrostomal tubules are formed by the
n of the walls of the pouch between two nephrostomes. The regions of
n extend in vertical lines from the nephrostomal margin of the pouch
y to its ventral border, where there is left an unfused and therefore
nuous longitudinal tract constituting the canal which I have called
ollecting trunk. This view of the development of the pronephros,
ugh suggested by Wilh. Müller ('75), was first described in detail
oette ('75) for Bombinator, and was later extended to other Am-
a by the researches of Fürbringer ('77). It has been entirely con-
d by Wichmann ('84), by Hoffmann ('86), and still more recently
arshall and Bles ('90^a).

In opposition to this view, I would maintain : (1) that the first
of the excretory system consists of a solid proliferation of somatop
the pronephric thickening ; (2) that the lumen of the system
secondarily ; and (3) that the pronephric tubules do not appear i
sequence of the local fusion of the walls of a widely open pouch
that they are differentiated at an early stage from the hitherto indif
pronephric thickening.[1]

The development of the pronephros and duct from a solid m
mesoderm was a common feature in the accounts of those who
prior to Wilh. Müller and Goette, but since then this mode of o
though repeatedly maintained by single observers, has failed to
general acceptance. Clarke ('81) described a solid pronephric thick
and asserted that the lumen arose secondarily in this mass ; the d
of the process are, however, not accurately given. Duval ('82
described the pronephros as first appearing in the form of a solid
ening. He however states that it later acquires a slit-like openin
the body cavity, and that by the imperfect closure of this openin
successive nephrostomes are formed, as described by Goette and
bringer. This latter statement I am unable to confirm. Gasser's
pp. 89–97) short note gives, on the other hand, an account of the
development in Alytes, which is in substantial agreement with m
observations. His account of the first differentiation of the nephros
canals is not very full, but it is not improbable that he conceive
take place in a manner altogether similar to that which I have desc
His statements seem to me in general correct,[2] but incomplete.

Janošik ('85, p. 19) states, on the basis of personal observations
the first trace of the segmental duct in Bufo and Triton is a solid
of cells, which he is, however, inclined to regard as a disguised f
somatopleure.

According to a recent account by Kellogg ('90), a lumen doe
appear anywhere in the organ (except in the region of the nephrost
until it has been separated from the peritoneum. Finally, Mollie
Rückert and Mollier, '89) has published an account of the early de
ment, which is for the most part in close accord with the results
own studies. Since these results were gained entirely independen

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[1] The large cavity which the pronephric pouch presents in Stage IV. of
and Bufo is a secondary condition produced by the expansion of the lumens
several diverticula.

[2] I must here except his statement that the second tubule is differentiated
the rest; this I believe to be an error.

ier's researches and were written out before his paper came into my ls, it seems to me that my confirmation of his position affords ex-nt evidence of the correctness of the view advocated. In one feature e our accounts of the earliest condition of the pronephros would seem ffer widely, but I am confident that the difference is apparent rather real. Mollier states that each of the diverticula which form the indications of the nephrostomal canals emerges from a protovertebral y. This statement, as I have already shown, does not in my opinion rately represent the actual conditions. In the stage under consid-on, the dorsal portion of the mesoderm is in the anterior region led by transverse planes into a series of metameric blocks; the pro-ric thickening also is made up of metameric constituents, and is inuous dorsally in Amblystoma with two, in Rana and Bufo with e, of the blocks of mesoderm. As yet no definite line can be drawn een the protovertebræ and the lateral plates; in a slightly older ryo, however, the protovertebræ begin to be constricted off from the al plates, and it is at once evident that the pronephric tubules have with the ventral segment of the mesoderm. This difference in our unts seems to me then very trivial, and my only excuse for dwelling it is the circumstance that Rückert and Mollier seem to attach great hological significance to this feature of their account. This relation e protovertebræ seems to me quite untenable.

revious authors have been singularly reticent respecting the exact ion of the pronephros with reference to the body somites. Für-ger ('78^{a}, p. 5) states that the pronephros of Anura extends over e, that of Urodela over two somites; but I have looked in vain for a ment which should show whether the nephrostomes are segmental or segmental in position. Kellogg states that each nephrostome occurs site the middle of a protovertebræ. Marshall and Bles confirm this ment, and contend that, in the case of Rana, the nephrostomes lie e 2d, 3d, and 4th somites behind the auditory vesicle. According ollier ('90, p. 213) the pronephros appears in Triton in the region e 1st and 2d trunk protovertebræ; but since the most anterior two overtebræ are reckoned to the posterior region of the head, these esent the 3d and 4th protovertebræ of the series. The enumeration h I have given for Rana and Bufo is in precise agreement with that arshall and Bles. For Amblystoma my account is in agreement that of Mollier for Triton.

am not aware that any definite attempt has thus far been made to rtain which of the three nephrostomes of Anura is unrepresented in

Urodela. At first sight it would seem probable, — and by implicatio accredit this opinion to Mollier, — that the rudimentary third tub occasionally present in Urodeles corresponds to the normal third tub of Anura. This view, however, is not in precise harmony with the r tions of the nephrostomes to the myotomes. As I have already sho the first nephrostome in Amblystoma is situated beneath myotome I whereas in Rana and Bufo it occurs under myotome II. If now enumeration of the somites in the two cases correspond, it follows t the first and second nephrostomal tubules of Amblystoma are equival to the second and third tubules respectively of Rana and Bufo, not their first and second tubules, and that the occasional rudimentary th tubule of Urodeles belongs to a more posterior somite, and is unrep sented in Anura. In Amblystoma the root of the vagus nerve ar immediately in front of the somite which I have denominated I.;[1] same is true in the case of Rana and Bufo, and I am inclined to reg these as equivalent somites. It is possible that somite II. of Amb stoma is not represented in Rana and Bufo; but this is hardly proba since it belongs to the head region, which is hardly likely to vary in s closely related groups, and since it is evident that the greater numbe protovertebræ present in Urodeles as compared with Anura is larg accounted for by additional protovertebræ in posterior regions, particula in the region of the mesonephros, as I believe. In general, it se to me that we should be more ready to admit the abortion of the m anterior tubule in Urodela than to assert the existence of an additio protovertebra in Anura.

All the more recent writers are agreed that in Anura three pair pronephric nephrostomes occur, Giles ('88, p. 135) alone claiming tha degenerating pronephros may have four. In Urodela the typical n ber is two; but Mollier ('90, p. 224) has recorded the occasional occ rence of three pairs in Triton, and I have made similar observations Amblystoma. Spengel ('76, p. 19, Taf. II. Fig. 21) maintained, on evidence of a specimen in which the pronephros was largely degenera that four pairs occur in Cœcilia; the recent observations of Semon (p. 462), on the other hand, have shown that there exist in Ichthyop on *each* side of the body ten *pairs* of nephrostomes, therefore forty in ne two nephrostomes belonging to any pair, one opens freely into the cavity, the other communicates with a pronephric chamber, which ains the glomus and is completely shut off from the body cavity. The ning of this condition I shall consider in the subsequent discussion. pairs of nephrostomes on each side are slightly more numerous than verlying protovertebræ.

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[1] Somite I. of this enumeration probably corresponds to the one which been called somite XI by Houssay ('91). Houssay believes that he can iden in Amphibia the somites which have been observed in the head region of Sela If his conclusions are accurate, they are evidence in favor of the view that region of the body is very permanent.

ne origin of the so-called ventral part (common trunk) of the pro- ros has recently become the subject of controversy. According to te the duct at first communicates with the posterior end of the widely pronephric pouch. At the same time that the nephrostomal canals ormed by local fusions of the walls of the pouch, a similar process ricts off the posterior ventral portion of the pouch; this has the of lengthening the duct, so that the point of its attachment is ed forward to the place where the converging nephrostomal tubes . The portion of the longitudinal canal in front of the most poste- nephrostome represents the "ventral part" of the pronephros.

cording to Fürbringer, the longitudinal groove which forms the st fundament of the pronephros and duct becomes entirely con- ed off from the somatopleure as far forward as the opening which into the pronephric pouch; this slit-like opening then elongates riorly, so as to extend into the region formerly occupied by the tudinal canal alone; the latter thus comes to lie ventral to the last rostomal canal, and forms the ventral part of the pronephros.

llogg ('90) opposes the accounts of previous observers, and claims the ventral part "is formed from the ventral side of the dorsal part e pronephros, and *anterior to the last nephrostome.*" Marshall and alluding to Kellogg's description, declare that it is in exact ac- nce with the accounts of Goette and Fürbringer. I have not been to satisfy myself as to the precise manner by which Kellogg con- s the formation of the ventral part to have taken place; but I think as said enough to contrast his position strongly with that of Für- er, according to whom the ventral part of the pronephros first ap- as a portion of the somatopleural fold immediately *posterior* to the which gives rise to the nephrostomal canals. Kellogg argues, how- that, were the views of previous authors correct, some portion of ronephros would appear behind the last nephrostome; but this is lly never the case. The force of this argument I am wholly unable preciate, and I must in consequence feel some doubt as to whether e properly interpreted Kellogg's previous statements.

cording to Mollier, the "ventral part" is differentiated in the ventral portion of the broad pronephric thickening. Mollier's des tion is substantially in accord with my own observations, and it s to me probable that Kellogg's statements are to be understood in same way.

The structure of the functional pronephros was early the occasic much controversy. The discoverer of the organ, Joh. Müller ('29 '30), describes and figures it as a cluster of blind tubules, which ra in the form of a rosette from the anterior tip of the segmental This view was shared by the larger number of the early investiga According to von Wittich ('52), the gland is typically formed by convolutions of a single tube; in the more complicated pronephr however, this canal may give off branches. It is to Goette and Fürbri that we owe the first accurate account of the process of convolution

According to these authors, the gland is composed of two portion "dorsal part" (collecting trunk and nephrostomal canals), which receives the nephrostomes,[1] and a "ventral part" (common trunk), w serves as the efferent canal, and is in communication with the ant end of the segmental duct. Both ventral and dorsal parts underg tensive convolutions, and give rise to blind diverticula. Subseq authors have in general confirmed Fürbringer's account, but have a no new matter to the description. Selenka ('82) describes and fig an interesting condition of the pronephros in Hylodes. The glan the two sides are unsymmetrical, and depart widely from the ty structure known in Amphibia. Following the nomenclature whi have proposed in the descriptive part of this paper, it is evident tha nephrostomal canals and the collecting trunk are present, but do show the convolutions customary in these parts. The "ventral part the gland, however, is not formed by the windings of the common tr but is composed of great irregular blind pouches which commun with the collecting trunk, while the latter opens *directly* into the terior end of the segmental duct. This condition of the pronephros dently represents the degeneration of the gland, and Selenka is incl to correlate the premature appearance of this complication in Hyl with the absence of gills in the larvæ of this form.

Kellogg has studied the structure of the pronephros in Amblyst and Rana by means of reconstruction from cross sections. His nary notice, however, does not describe the process of convolution in ail. An interesting feature is the statement that blind diverticula do appear until the tubes of the gland have become very much convo- d. In the pronephridia which I have studied, I have never seen a d diverticulum. My observations do not extend to sufficiently old es to allow me to deny that such diverticula appear anywhere in the elopmental history of the gland, but the organ can reach at least the degree of complexity shown in Figures 41 and 65, and yet be com- ed of the windings of the nephrostomal canals, the collecting trunk, the common trunk without possessing any blind diverticula.

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[1] Duval ('82, Fig. 7), figures the second pronephric nephrostome in Rana as ing directly into the ventral part of the gland. I have never seen such a cond in my preparations, nor do I know of similar observations being elsewhere reco It seems likely that Duval has here fallen into error.

t is needless for me to discuss in this place the histology of the tubu- portion of the pronephros. These details have little general interest, they have furthermore been accurately given by Fürbringer and fmann ('86).

he dilated chamber which I have described (page 240) was also ob- ed by Hoffmann, but he was unable to determine what portion of the em was concerned in its formation. Similar dilated chambers are wise described by Marshall and Bles, who regard them as steps in degeneration of the tubules. The early appearance of these dilated ons in Rana (see page 232) seems to me to render this interpretation robable.

ccording to the usual account, the capsule arises as a differentiation he connective-tissue stroma, which lies between the pronephros and ectoderm. Duval ('82, pp. 25, 27) alone has claimed an origin from overlying protovertebræ; but, singularly, his statement has been lly neglected by subsequent writers. His observations on this point e in all essential features with my own.

he glomus was discovered by Joh. Müller ('30, p. 12), but the sig- ance of the structure was wholly problematical until Bidder ('46, p. suggested its glomerular nature, which has since received general ptance. This view has, however, been opposed by Semper ('75, pp. *et seq.*), and more recently by Hoffmann ('86, pp. 572, 573). Accord- to Goette and Fürbringer, the glomus arises as an outfolding of the nchnopleure opposite the pronephric nephrostomes. The interior of fold becomes occupied by mesenchymatic cells and with blood tracts, ch communicate with the aorta. According to Hoffmann, the inte- is largely occupied by "columns" of large cells, which would seem ign to the nature of a glomerular structure. These 'columns of cells," ays, may be seen to arise, in Bufo at least, by the invagination of the erficial covering of the glomus. I have myself seen continuous cylin-

drical cords of cells in the glomus; but in most cases I have been re
able to satisfy myself that this appearance had to do with densely pa
blood cells lying in a definite vascular tract. I have also occasio
met with invaginations of the superficial (peritoneal) epithelium o
glomus (page 247); but it seems to me, even should it be shown
they give rise in the interior to columns of cells, that this would no
a very serious objection to the view which ascribes to the organ a
merular function. In favor of that view, many arguments may b
duced: (1) the highly vascular nature of the glomus; (2) its pos
in an open chamber of the body cavity directly opposite the prone
nephrostomes; (3) its serial relations with the mesonephric glome
(4) its appearance and degeneration synchronously with the pronep
and (5) the circumstance that its homologue, wherever found in
classes of Vertebrates, is always in equally close relation with excr
tubules. The last argument seems to me the most weighty, and I a
opinion that a comprehensive comparative study proves beyond que
the glomerular nature of the structure.

In the descriptive part of this paper I have stated that, in satisfa
sections through the blood-vessel which leads from the aorta to the glo
one could frequently observe that the ramifications within the gl
did not appear to be terminal, but that the vessel seemed to giv
a lateral branch to the glomus, while the main trunk continued o
ward the ventral side of the body. An explanation of this conditio
occurred to me, which, if confirmed, will be of considerable morpholo
significance, though at present I can merely offer it as a suggestion.
we have already seen, the glomus of Selachii, according to Rückert
pp. 239–242), does not receive a separate blood-vessel directly from
aorta, but a rete mirabile is developed in connection with the segm
vessels described by Paul Mayer. I have not succeeded in tr
the main aortic branch to the ventral side of the larva; but, as far
could be followed, the course of the vessel between splanchnopleure
entoderm corresponds perfectly with that of one of the segmental
sels described by him. It seems to me quite possible that, in Ampl
the dorsal portion, which is in communication with the glomus, is
only part of these rudimentary vessels which is retained, and that
remaining portion, having ceased to be of functional importance, fa
develop.

Having completed my survey of our knowledge of the developme
the pronephros in the several classes of Vertebrates, I now turn

ideration of the development of the segmental duct. As is well wn, observers up to a very recent date have been almost unanimous scribing a mesodermal origin to this structure. In regard to the ils of the process, however, they have been less at one; and I shall rdingly treat of their accounts under three heads, which seem to me present fairly well marked phases of opinion.

ccording to one view, *the duct arises as an evagination of somatopleure, umen being therefore a detached portion of the body cavity.* Such a e of origin was advocated by Rosenberg ('67, pp. 42 *et seq.*) for osts; and this feature of his account has gained almost universal ptance both for Teleosts and for Amphibia, having been recently ely confirmed by Hoffmann ('86) and Henneguy ('88, '89). According to Wilh. Müller ('75) and Fürbringer, the duct arises in this way in Petromyzon, and a similar claim has been made for Ganoids by alewsky, Owsjannikow, and Wagner ('70), and by Balfour and Parker). In Selachians, however, the weight of the evidence is distinctly sed to this view, and I am not aware of its having been advocated ny one besides Schultz ('75).

Amniotes also such an account of the early development has not ved general acceptance; it was first claimed in this class by Romiti), and was adopted, with some modification it is true, by R. Kowaky ('75), and by Dansky und Kostenitsch ('80, p. 24). Very rey such a mode of origin has been reasserted by Fleischmann ('87) arnivores and the Duck.

y own observations on Amphibia indicate that in this group the does not arise as a fold; and I am of opinion that, in both Cycloes and Ganoids, the evidence that the duct arises by evagination is resent unsatisfactory. It seems to me probable, on the contrary, the method of origin which is usually recognized as characteristic of he Anamnia with the exception of Selachii exists, if at all, only in osts. In view of the peculiar obstacles which Teleostean material nts for embryological study, one should be cautious in affirming for group a mode of development which, in my opinion, is not proved to in any other class of Vertebrates.

second view of the origin of the duct is, that it *arises from a solid feration of somatopleure.* According to Fürbringer ('78^a), Spoof ('83,), and the earlier writers (Remak, '55, Kölliker, '61, Bornhaupt, Waldeyer, '70, and Foster and Balfour, '74), the duct arises in the by a proliferation *in situ* of the subjacent mesoderm, and a similar n is maintained for Petromyzon by Scott ('82). The more recent

view, however, affirms that the posterior end of the duct grows
ward free from adjacent tissue, the cellular material being whol
rived from an anterior proliferation. For Selachii this method of
has been maintained by Balfour ('78), and for Amniotes by a large
ber of observers; e. g. Weldon ('83) and Mihalkovics ('85) in Re
Gasser ('77), Sedgwick ('81), Schmiegelow ('81 and '82), and Janošik
in Birds; Renson ('83) and Martin ('88), in Mammals. Gasser
believes that the segmental duct in Alytes has no direct connectio
the mesoderm, posterior to the pronephros; but he was unable
clude with certainty the possibility that the somatopleure immed
behind the pronephros might take some part in the formation
duct. Mollier ('90, p. 226) moreover asserts that such a partici
actually takes place in the two somites following those in which th
nephros is formed, but that the posterior portion of the duct pr
grows back from this point independently of the mesoderm.

In so far as these authors maintain that the duct arises from
proliferation of mesoderm and acquires its lumen secondarily, I e
agree with them; but my observations on this point lead me to co
further that the duct arises throughout its entire length from a co
ous thickening of somatopleure, and that the only free growth
occurs in the Amphibia studied by me is for the purpose of effec
union with the cloaca. In assuming this position, I am aware of
in conflict with prior observations on Amphibia, and with the more
accounts of the development in other groups; it seems to me, ho
that satisfactory evidence in favor of this mode of origin has be
duced in the descriptive part of this paper.

Finally it remains for me to consider the third view, that of the
dermal origin of the duct, which is to-day advocated on so many
As early as 1855 Remak expressed himself as dissatisfied with the d
tion of the excretory system from the mesoderm, although this mo
origin was confirmed by his own observations. A decennium late
('65^b, pp. 160–162) maintained that, in the Chick, the Wolffia
Müllerian ducts both arise as folds of the ectoderm; but he aban
this position later ('68, p. 119), when it had been shown by Born
('67) and Dursy ('67) to be untenable. He then endeavored to int
the facts in harmony with his theoretical conceptions by maintainin
the cells from which the Wolffian and Müllerian ducts arose wer
marily derived from the ectoderm, a view which was likewise adopt
Waldeyer ('70). Meantime Hensen ('66) had indorsed the view
direct origin from the ectoderm. He states ('66, p. 81, foot-note)

the Rabbit the Wolffian duct arises from a solid rod-like thickening of
e ectoderm near the middle protovertebræ. In a second short commu-
cation ('67, p. 502), Hensen merely reaffirmed his confirmation of His;
it finally he ('75–'76, pp. 369–372) published a fuller account of his
servations, accompanied with figures. These, however, are far from
nclusive, and it does not seem surprising that this single observation
as distrusted by subsequent writers.

In 1884 Graf Spee published an account of his very careful investiga-
on of the subject, and reasserted the ectodermal origin of the Wolffian
ict.[1] Following this publication have appeared a large number of con-
matory papers, which have moreover extended the observations of
raf Spee; so that at present the ectodermal origin of the duct has
en asserted for every class of Vertebrates, with the single exception of
e little known Dipnoi.

As stated in the Introduction to the present paper, it was my hope
undertaking these studies to find in Amphibia results confirmatory of
raf Spee's position. If, then, a contrary result has been reached, it
s been because I have been driven to that conclusion by evidence
ought out in the course of the investigation. In my opinion, the
tire excretory system of the forms I have studied unquestionably
velops without any participation of the ectoderm in its formation.
ie duct develops from mesoderm throughout its entire length, and
its posterior end, in Rana and Bufo at least, comes in contact with
e of the entodermal cornua of the hind gut; so that *nowhere* in its
velopment does it come into organic union with the outer germ
yer.

I must in this case distinctly disavow the suggestion of Hertwig ('88,
280), who endeavors to harmonize the accounts by assuming that
ly the posterior end of the duct is formed from the ectoderm. This
planation would by no means be admissible, unless it be granted that
e ectodermal constituent might in this case be reduced to nothing
all. On the other hand, it must be confessed that a fundamental
position in the mode of development of an organ in two closely related
oups is at present hardly reconcilable with our general conceptions
embryological processes.

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[1] Graf Spee, and subsequently Flemming ('86), did not clearly recognize the fact
at the Wolffian duct and the mesonephros develop in different ways, and were
l to defend an ectodermal origin for the *excretory system*. This interpretation is in
ident opposition to the accounts of others, and, in my opinion, is not justified by
eir own observation, even should these prove to be accurate in every particular.

It will therefore be of interest to review critically the most r accounts in the several groups, for the purpose of ascertaining wh the ectodermal origin of the segmental duct be in any case act demonstrated. For this purpose, only those papers which hav peared since Graf Spee's researches need concern us. Of these larger number are brief notices, which, in view of the extreme diffi of the investigation, cannot be regarded as conclusive.

In regard to Cyclostomes, the only papers that have appeared d this period have been preliminary notices; that of Kupffer ('88) tains an ectodermal, those of Goette ('88) and Owsjannikow (' mesodermal, origin for the duct.

In Teleosts, the duct has been claimed to be ectodermal by ('87) and Ryder ('87); but on the basis of my own observations, are as yet incomplete, I am led to doubt the correctness of this c which has already been opposed by the observations of Henneguy of H. V. Wilson ('90), and of McIntosh and Prince ('88). In account by Brook, it seems to me probable that the ectodermal t ening observed has in reality a very different significance (lateral proliferation) from that attributed to it, an opinion which is shar Wilson ('90, p. 58). The only recent paper dealing with the dev ment of the Ganoidean excretory system is the preliminary notice of ('89) on Lepidosteus. According to Beard, the duct is ectodermal.

In Amphibia, also, an ectodermal origin of the segmental duc been asserted by Perenyi ('87) and by Brook ('87). Their com cations, however, are both short notices, and in the absence of the papers cannot be regarded as satisfactory evidence. Moreover, the dermal origin of the duct has been reaffirmed by Mollier ('90), Ke ('90), and Marshall and Bles ('90).

It is rather remarkable, that, in all the preceding classes, nothin preliminary notices have ever appeared in favor of the ectodermal The same is true of Birds, where this mode of origin has been cla as probable by Beard ('87) and by Brook ('87). On the other a number of observers have carefully investigated the chick with special purpose in view, and have been unable to find any evidenc participation of the ectoderm in the formation of the Wolffian Among these may be mentioned Janošik ('85), Mihalkovics ('85) Hoffmann ('89). Peculiarly significant, however, is the fact that Spee ('86) was unable with the use of the most various reagents t any direct evidence of a genetic connection between the ectoderm the Wolffian duct in the *Chick*.

n Reptiles, a number of writers have asserted that the Wolffian duct
es from the ectoderm. According to Perenyi ('87, '88, '89), irregu-
groups of cells are at an early stage budded off from the ectoderm
ering the middle plate, and on the first formation of the segmental
icles they form the cord of cells which has been recognized by prior
ters as the fundament of the duct. In my opinion, no conclusive
lence is adduced to prove that the cells figured in the latter position
), Fig. 5, *ceW.*) are descendants of those which at an early stage
n part of the ectodermal thickening. Mitsukuri ('88) and Orr ('87)
e published short notes claiming an ectodermal origin for the duct;
, finally, Ostroumoff ('88^{a}, '88^{b}) asserts that it is derived from the
oderm in Phrynocephalus. It seems to me, however, that Ostroumoff's
ervations are incomplete at a critical point, and that no satisfac-
y evidence is brought forward to show that the ectodermal thick-
ngs which he describes and figures ('88^{b}, Tab. III. Fig. 56) with all
irable clearness, are unquestionably the fundament of the Wolffian duct.
ey may be merely chance thickenings over the intersegmental depres-
ns in the underlying mesoderm. On the other hand, Mihalkovics
5), Strahl ('86), and Hoffmann ('89) have all sought in vain to find
sfactory evidence of a participation of the ectoderm in the formation
he Wolffian duct.

Vith all the preceding classes of Vertebrates, I am of opinion that
weight of evidence is at present in favor of the view that the excre-
y system is wholly derived from the mesoderm. For the remaining
ups, Mammals and Selachians, however, no such claim can be sus-
ned. The researches of Graf Spee on Cavia showed conclusively
t a cord of cells representing the fundament of the Wolffian duct is
tinuous posteriorly with a ridge of tissue which is still in intimate
on with the superficial ectoderm, and that, in the further develop-
nt, a continuous cord of cells separates off from this ridge by the pro-
ssive formation of a split between the deep portion of the ridge and
superficial ectoderm. At first, a distinct membrana prima is reflected
n the unmodified ectoderm over the ridge, and the partially separated
dament of the duct may still be in connection with the superficial
oderm by means of such a membrane. This latter feature is also
lt upon by Flemming ('86), who furthermore emphasizes the cir-
nstance that in the ridge which forms the first rudiment of the
lffian duct mitoses are especially abundant, and that the nuclear
ndles are frequently perpendicular to the surface, i. e. are so situated
t the ensuing cell divisions would tend to thicken the layer. The

general results of these two investigators have been confirmed by B ('87 and '88) in the Dog and Sheep, and a number of former adv of a mesodermal origin have satisfied themselves of the correctness opposed view by a study of the preparations of these authors; e. (see Spee, '84, p. 93), Waldeyer (see Janošik, '85, p. 13), and Mihall (see van Wijhe, '89, p. 501).

The most recent paper on this subject is that of H. Meyer ('90) claims an ectodermal origin for the Wolffian duct in man. The e upon which these observations were made was obtained by art abortion, and was at once preserved by histological methods; so in the opinion of the author, it would be unfair to ascribe his resu imperfect preservation, which so frequently renders observatio human material untrustworthy. On the other hand, the mode in the duct is here claimed to originate, viz. as a conspicuous *fold* o derm, is so different from the method of origin described in other mals that one cannot regard this observation based on a single spe as conclusive evidence.[1]

A few recent writers have reasserted the mesodermal origin Wolffian duct even in the case of Mammals. Lockwood ('87, p. 642 icises the evidence adduced by Graf Spee and Flemming, and com their ectodermal ridge to a number of insignificant ectodermal thi ings which may be observed over depressions in the underlying tis diverse regions of the body. Lockwood entirely ignores the very nite relations which Graf Spee showed to exist at a certain stage be the fundament of the duct present in anterior regions and the conti posterior ridge; his entire criticism therefore seems to me quite u ranted. Fleischmann ('87) also reasserts in a preliminary note the dermal origin of the duct in Carnivora; but his description of the of origin is so entirely at variance with the accounts of recent autho that his statements can hardly be regarded satisfactory before the evi on which they are based is produced.

On the other hand, Martin (Stahl und Martin, '86, Martin, '88) a the main features of the development as described by Graf Spe nming, but interprets their observations in a fundamentally different . In the course of a painstaking investigation, in which more than y series of sections were used, Martin never encountered conditions ch in his opinion demonstrated a genetic connection of the duct with ectoderm. He believes that the duct arises from a proliferation of oderm in the region between the 9th and 11th protovertebræ, and vs backward by cell division within its own mass. The posterior ion of the duct, however, fuses with the ectoderm so intimately that ertain regions it is quite impossible to recognize a boundary between n; but Martin believes that the fusion is wholly secondary, and that ectoderm contributes no material to the duct. Keibel's ('88^a, p. 635) lies on Erinaceus led him at first to accept Martin's attempt at har- izing the two views; but in Cavia ('88^b, pp. 424–428) his observa- s inclined him towards the original view of Graf Spee.

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[1] During the correction of these proof-sheets another paper has appeared asserts a participation of the ectoderm in the formation of the duct in Man (Koll '91). In the region of the middle plate there is found, according to this aut close fold of ectoderm (Taf. III. Figs. 3, 4, *Anlage d. Urniere*, Fig. 8^{a}) whi believes to be concerned in the formation of the duct, thus confirming Meyer' account. The later stages studied by Kollmann, however, are too far adv to afford convincing evidence that his interpretation of the fate of this f accurate.

n my opinion, Martin is right in denying that an ectodermal origin of Wolffian duct has been demonstrated in Mammals. It is undoubtedly , that there is considerable evidence in favor of such a mode of origin; it is not of a nature that would warrant one in concluding that the arises in this way throughout all Vertebrates, or in asserting that velops in fundamentally different ways in Mammals on the one hand, in other Vertebrates on the other. All that can be claimed, how- , in accordance with Martin's view, is that it is possible to interpret conditions in Mammals in agreement with observations in other Ver- ates, should these be shown to be less ambiguous.

n Selachians, the evidence in favor of an ectodermal origin of the is perhaps even stronger than in Mammals. In the former group, des the preliminary communications of van Wijhe ('86, '88^a) and rd ('87), there have appeared two extensive papers by Rückert ('88) van Wijhe ('89), which seem to place the ectodermal origin of the nental duct almost beyond question; and, so far as I am aware, no nt observer has expressed doubts upon this point. It nevertheless ns to me that, before accepting this result as final, we have yet to ire whether Martin's interpretation of the condition in Mammals not be applied also in Selachii.

might be objected, that the latter view offers no explanation for the nate fusion which must be granted to exist between the posterior end he segmental duct and the ectoderm; yet this argument cannot in- date the general conclusion, since a number of cases of such a union vo epithelial structures in their growth have been recorded, where genetic connection is believed to exist. Such a conception is involved, for example, in the account — contested, it is true — given by Carius ('88) of the anterior growth of the chorda in the "Kopffortsatz" of Cavia, the chorda being in intimate fusion with the underlying entoderm; or, again, the backward growth of the Amniotic Müllerian duct in close connection both with the Wolffian duct and with the adjacent peritoneum, as described by a number of recent writers.

In conclusion, then, I am of opinion that the more primitive condition, and that shown by most Vertebrates, is the development of the segmental duct independent of connection with the ectoderm; but that in certain groups the duct enters into a secondary union with the ectoderm. The question whether the ectoderm here contributes material to the fundament of the duct can at present receive no more definite answer than that contained in the foregoing discussion.

It has frequently been asserted that the mesodermal origin of the kidneys is not in harmony with our conceptions of the derivatives of this germ layer. As early as 1855 Remak saw a fundamental opposition in the mode of development which he described for the excretory organs, and that familiar in the case of other glands. According to his view, which received very general acceptance, the kidney is a unique example of a gland whose secreting surfaces are not derived from one or other of the bounding germ layers, ectoderm and entoderm.

In my opinion, this view must now be considered inaccurate. It is doubtless true that glands are usually developed either from the ectoderm or from the entoderm; this circumstance may merely be due to their apparently being seldom needed on mesodermal surfaces. Certain special regions, however, seem to require glands. Such regions are the sexual conduits in which, besides those glands which have special functions, such as the deposition of the secondary egg membranes[1] (Ludwig), we should expect to find glands similar to those which are found in the course of other canals leading to the exterior, such, e. g., as the trachea. I shall disregard the glands which develop in the ampullæ of the vasa deferentia, since these are derived from the Wolffian duct and consequently *may* be of ectodermal origin in Mammals, and shall take as a specific example the genital tract of the human female. It seems very certain that in Amniotes the Müllerian duct develops entirely independently of the Wolffian duct, as an evagination of the peritoneal covering of the Wolffian body. Moreover, whether we accept the view of van Ackeren ('89), that the hymen marks the region of fusion between the fused Müllerian ducts and nus urogenitalis, or that of Nagel ('89), who claims that the vagina product of the sinus urogenitalis, the boundary between the two ituents being marked by the os externum uteri, it must in either be granted that the entire genital tract from the ostia abdominales oviducts to the os externum is of mesodermal origin. This entire n is lined with a continuous columnar epithelium, which is con- us below with the stratified epithelium of the portio vaginalis. In istological characters this membrane closely resembles a typical us membrane, and is subject to the characteristic disorders of this of tissue, cancer and catarrh. The Fallopian tubes are believed to thout glands;[1] in the region of the fundus and corpus, however, are rous long tubular cœcæ which have been called uterine glands. It ot been demonstrated, however, that these structures exercise a ory function; and they may merely serve to regenerate the mucosa in menstruation. In the cervical region occur glands (glandulæ thi, Schleimkrypten) which are much shorter than those in the of the uterus. These cervical glands secrete a viscous fluid of the cteristic ropy consistency of mucus, which at periods mingles with atamenial flow,[2] and, in certain stages of pregnancy, forms a com- plug in the cervical canal. This secretion forms a dense mass on on of alcohol; it swells conspicuously when placed in water; it blue with hæmatoxylin, and pink with picro-carmin; and, finally, ding to Overlach ('85) its formation is attended with the same mental changes in the protoplasm at the distal end of the secreting which are familiar in the case of ordinary mucous secretion.[3] It most certain that the cervical glands produce true mucus. Not y, then, does the mesoderm give rise to glands, but *it produces of the same nature as those found in mucous passages of ecto- l origin.*

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[1] The albumen secretion of the Hen's oviduct is a familiar example. According to Giacosa ('72) the oviducal secretion in Rana is largely composed of mucin.

econd view was that formulated by His ('65^a), according to which

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he vagina also is stated by Veith ('89) to be normally glandless.

f interest in this connection are the observations of Artemjeff ('89), who bes mucous corpuscles as a constituent element of normal lochia.

hrough the kindness of Dr. C. S. Minot, I have been able to try in addition simple chemical tests on the cervical secretions. The cervical plug from a of three months' pregnancy examined by me, proved to be soluble in po- sodic, and calcic hydrates, and in sodic carbonate; it is precipitated by acid, but redissolves in excess; in strong acetic acid, on the contrary, it s not to redissolve. The substance gives the proteid reaction with nitric ut not that with cupric sulphate. It also gave the specific mucin stain with len blue recommended by Hoyer ('90).

the ectoderm and entoderm alone are capable of giving rise to ep tissues. This view, which was associated with the derivation urogenital tract from the ectoderm, was naturally revived by Gr ('84). More recent evidence, however, shows that it is only the duct in regard to which the question of an ectodermal origin open; the Wolffian tubules, on the other hand, as well as the e of the female sexual tract, are distinctly mesodermal. The sta that epithelia do not arise from the mesoderm is, in my opinion insignificant or untrue. If, avoiding genetic characters, we defi thelium so narrowly as to exclude endothelium, we must confes except in certain specialized regions, epithelia do not develop fr mesoderm; but the conclusion is obviously of little morphological tance. On the other hand, if we employ broad morphological cha in our definition, such a conclusion is manifestly inaccurate.

The ectodermal origin of the Wolffian duct has been supp account for certain pathological new formations which frequent their seat in the urogenital organs. Thus His ('65^b) saw in the development which he described for the Wolffian and Müllerian d explanation for the occurrence of dermoid cysts in the ovary. be confessed that the structure of many of these cysts suggests th have an ectodermal origin; but their occurrence in very diverse the body shows that they do not require a normal ingrowth of ecto cells into the region in which they arise. Thus in the dermoi which are occasionally found back of the optic bulb, the transl must be regarded as purely adventitious.[1]

The suggestion has recently been made by Sutton ('86, p. 34 testicular and ovarian carcinomata are to be explained by the occ of degenerating ducts in the neighborhood of the genital ridge, ar inclined to regard the Wolffian duct as the means of transportin dermal cells to this region. The weight of evidence seems to fa view that carcinomata cannot develop without an epithelial basis '89, p. 771); but this fact does not compel us to seek an ecto source for these growths. In the case of adenomata, which also an epithelial basis, one can see more readily the source of the p tion; and these abound in the ovary. The germinal epithel consequence of its retention of embryonic characters, seems to adapted to the formation of carcinomata, and, according to Birch-feld's ('89, p. 202) enumeration, they are somewhat more frequen

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[1] Many dermoids may be explained as cases of *fœtus in fœtu*, and thos ovary may often be due to extra-uterine gestation.

y than in the testis, even though the latter organ is in such intimate
tions with degenerating Wolffian canals.

he remaining portion of the present paper will be concerned with
e inferences of a general nature which can be drawn from the develop-
t of the pronephros and segmental duct as traced in the preceding
s. These general conclusions naturally fall into two groups : (1) such
re of principal interest in elucidating the development of the excre-
system, and (2) such as tend to throw light on the development of
Vertebrate type. Following this division, then, in our discussion, I
l consider in the present section the organogenetic conclusions; and,
ncluding, deal with the phylogenetic conclusions which seem to me
ranted by our present knowledge.

n the historical review of the development of the pronephros, it proved
everal groups very difficult to draw a sharp line between the pro-
ros and the mesonephros, and it was suggested at that point in the
ssion that this difficulty is in reality a fundamental one, and one
h is indicative of the true relations between these parts. The
tion of the serial homology of the pronephros and mesonephros, as
resents itself to the modern student, is to my mind simply this:
we to regard these two glands as derivatives of one continuous
stral organ, which at one time extended over all the somites now
pied by each? The answer to this question naturally must come, if
l, by a comparison of the two organs for the purpose of bringing to
their features of similarity and those of contrast. Manifestly they
r in the time of their appearance; indeed, from this circumstance
two glands were distinguished and named; it remains to consider
ther they are constructed on the same or on different types.

endeavoring to furnish an answer to this question, I shall proceed
n anatomical comparison of the glands, taking into consideration both
he principal portions involved, the glomerular and the tubular parts.

glomerulus of the mesonephros resembles the glomus of the pro-
ros in the following particulars: both are highly vascular structures
posed of ramifying blood-vessels and mesenchyme; they project into
es which are in communication with the exterior by means of excre-
conduits; they originate outside of this space, and gain position
in it by pushing before them in their growth its epithelial wall, which
persists as an outer covering to the vascular process; they receive
ches directly from the aorta; and, finally, they are developed in re-
s of the body which at least nearly correspond to each other serially,

as is shown by the relations of the glomus and the glomeruli respec to the aorta, and by the existence of transitional glomeruli (Birds, odilia, Chelonia). On the other hand, the features in which the g differs from the glomerulus may be summarized as follows: the g lies in the body cavity, instead of projecting into the lumen of cialized excretory tubule, and it is a continuous structure, inst consisting of a number of separate parts.

Turning now to the tubular portions of the two glands, one can nize a number of common characters. In both can be distinguis longitudinal conduit and transverse canals, the latter communicatin the body cavity by means of ciliated nephrostomes. The longit canal of the two glands is in reality a continuous structure, the segn duct. Since the pronephric and the mesonephric tubules are sin related to this continuous duct, it is evident that they must them lie in approximately equivalent regions of the body. The metan of both glands primitively corresponds to that of the body somites feature is apparent from my account of the Amphibian pronephro has been proved for the most anterior mesonephric tubules in A stoma (see page 261), as well as for the entire series in Selachii an tain other groups. Finally, the cardinal veins give rise to a meshw vascular spaces which bathe in a like manner the tubules of the pr ros and mesonephros. In addition to the different ways in which tubules are related to glomerular structures, the pronephros and nephros are unlike, in that the tubules of the former develop in cont with the duct, while those of the latter join the duct secondarily. character of the convolution also is different in the two glands. evident from the reconstructions (Plates IV. and VIII.) of the prone in Rana and Amblystoma, the complication is here mainly due convolution of the longitudinal canal (common trunk); whereas i case of the mesonephros the longitudinal canal (segmental duct) tra the gland as an almost straight duct, the transverse tubules alone highly convoluted.

The pronephros and mesonephros, then, present many striking tomical features of resemblance, but also differ in several respec am however of opinion, that the similarities of structure are suffic great to make it probable that pronephros and mesonephros hav veloped from a common beginning. I do not think, however, that tabulation of the resemblances and differences gives an adequate i into the true relationships of the structures. In the search for tral characters, it is a matter of indifference whether the organ in

actually realizes a given character, or merely shows a tendency to
ne it, provided in the latter case it can be satisfactorily shown that
realization of the tendency was prevented by intelligible causes.
, in the gastrulation of meroblastic eggs, if it be recognized that
great accumulation of yolk renders emboly impossible, the substi-
n of epiboly in these cases must be regarded as morphologically
nificant.

ie question now naturally arises, Are any of the contrasts between
ephros and mesonephros of such a nature that they can be explained
e result of a single modifying influence? As I have already stated,
nost marked point of disagreement between the two glands is the
ence in time at which they appear. What influences may that
r exert in modifying their development? At the time when the
hibian mesonephros appears, the myotomes are widely separated
the peritoneum, and the continuous strip of cœlom immediately
al to the lower boundaries of the protovertebræ in the region of the
ephros does not exist in the region of the body in which the meso-
ros develops. In its place is a mass of cells which extends from the
l angle of the body cavity upward towards the overlying myotomes.
mass of cells has been regarded as the first rudiment of the meso-
ros. The most natural explanation of the condition is that this mass
lls is morphologically not a secondary proliferation from the perito-
, but is really the last remnant of the mesoderm which formerly
ected the dorsal angle of the permanent body cavity with the over-
protovertebræ. The correctness of this interpretation is shown by
arison with the conditions in Selachians and in Amniotes, where,
ding to the mutually confirmatory accounts of Sedgwick ('80^a), Van
e ('88^a, '89), Rückert ('88), and Hoffmann ('89), the mesonephric
les develop from the communicating canal. The first rudiment of
mesonephric tubule is in reality that portion of the primitive meso-
al plate which lies immediately ventral to the protovertebræ, and,
sponds to that portion of the cœlom into which, as shown in Figure 6,
glomus projects, and from which the pronephric tubules emerge.
mesonephric fundament, then, presents on its outer side somatic, on its
, splanchnic mesoderm. When the fundaments of the mesonephros
been converted into a series of blind tubules, they grow outward and
the segmental duct. This process appears to me to be precisely
valent to the *somatopleural* evagination, which at an early period gave
n the anterior region to the nephrostomal tubules of the pronephros.
portion of the differentiated mesonephric tubule into which the

glomerulus projects is of different origin; it is merely a portion cœlom, the walls of which are to be understood to be formed as I just stated in part by somatic, in part by splanchnic mesoderm.

Returning now to the two features in which the glomus was to differ from the glomeruli, — viz. situation within the body cavit continuity throughout successive somites, — it will be seen that it possible to maintain the former as a ground of distinction, sinc glomerulus also lies in a detached portion of the cœlom, and th latter ground is equally untenable because it simply results from th that, before the glomeruli appear, the space into which they would wise project as a continuous organ has already been broken up series of distinct tubes; the glomerular organ is consequently b up into a corresponding number of separate vascular processes, e which becomes converted into a Malpighian capsule.

It seems probable, therefore, (1) that the pronephros and mesone were primitively alike, and were portions of a single continuous g (2) that in Vertebrates which came to lead an independent exi early in life, an anterior portion of the gland and the whole of the are differentiated before the posterior part for the immediate purpo the larva; and (3) that the difference in structure between th glands is mainly due to their arising at different times relatively differentiation of the body cavity and protovertebræ. Applyin conclusion to the tubular portion of the glands, it becomes at once ligible why the tubules of the mesonephros must of necessity joi duct secondarily. From this standpoint, the existence of convol in the common trunk points to a less differentiated condition pronephros, in that, for temporary purposes, the longitudinal including the common trunk, subserves at the same time the fun of an efferent duct and of a secreting tubule.

The foregoing explanation of the nature of the pronephros is upon the assumption that it is developed as a larval excretory In order to justify this position, it will be necessary to consider wl the pronephros is functional in those Vertebrates which, viewed fron standpoint, would seem to require this organ, and in such alone. the present purpose, two methods of sexual reproduction may b tinguished: (1) that in which the mother spends her energy in prod a large number of offspring, which are early forced to care for thems and (2) that in which the mother produces a small number of eggs either by giving to each a large quantity of reserve food yolk, nourishing the young embryo within her own body, secures the exis her offspring without calling into play their individual activities. In e former class may be reckoned Cyclostomes, Teleosts, Ganoids, Dip- i, and Amphibia.[1] Omitting from consideration the little known pnoi, a functional pronephros appears in all the members of this group thout exception, and is most highly developed in those forms (Petro- zon, Amphibia) which pass through a protracted larval stage. The ier class includes Selachians, Reptiles, Birds, and Mammals. In every mber of this group the pronephros is rudimentary.

I conclude, therefore, that pronephros and mesonephros are parts of one cestral organ; that the glomeruli are strictly homodynamous with the mus; that the entire tubular portion of the pronephros is represented in mesonephros; that the cavity of a Malpighian capsule and the nephro- nal canal connecting it with the body cavity are detached portions of the om, the equivalents of which are not thus differentiated in the pronephros; t the pronephros is developed as a larval excretory organ; and that the iod at which it appears largely accounts for its peculiarities of structure. is general conclusion, which is mainly based upon a study of the con- ions in Amphibia, is, in my opinion, in perfect harmony with the orded observations on other groups.

It must be remembered in this connection, however, that the pro- hros may possibly have been developed from the primitive excretory an independently in two or more groups, in response to similar physio- ical necessities. While I have not been able to preclude this possibility, m nevertheless inclined to the opinion that in general a closer relation sts, and that consequently the pronephros is homologous throughout Vertebrates. An interesting condition manifests itself in those forms leosts and Ganoids) in which the pronephros remains functional until individual is nearly adult. In these the pronephric chamber becomes tially (Lepidosteus) or entirely (Teleosts) cut off from the body cavity comes to resemble an enormous Malpighian capsule. The region in codilus intermediate between pronephros and mesonephros shows a

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In the one group, the eggs are holoblastic, or if meroblastic contain little yolk leosts); in the other, they contain much yolk, or the young are nourished by ns of a placenta (Mammals). Mr. Samuel Garman has kindly called my atten- to a number of cases in Amphibia where the period of larval life is greatly iced. The occurrence of holoblastic segmentation in this group appears to to afford adequate evidence that such conditions are secondary. Moreover, e actually appears to be a reduction of the pronephros in such species as ndon in part their larval life. In the case of Hylodes martinicensis, mentioned Mr. Garman in this connection, Selenka ('82) has shown the pronephros to very degenerate.

similar differentiation of a part of the cœlom into a distinct excr chamber. The condition in this region differs from that of the nephros of this genus solely in the circumstance that the excretory ber is not broken up into metameric portions; this process takes in the posterior region, and produces a typical mesonephros.

It now remains for me to review the opinions of previous writ respect to the nature of the pronephros. The existence of a larval tory system different from and earlier than the mesonephros appe have been first suggested by Marcussen ('51); but this view receiv recognition until it had been reasserted by Wilh. Müller ('75), who to the pronephros a distinctive name, *Vorniere.* Semper ('75), o other hand, denied utterly the nephridial nature of the pronephro regarded the glomus as equivalent to the suprarenals (Nebenniere Plagiostomes. Fürbringer ('78ᵃ) vigorously opposed this view, and tained that the pronephros and its duct represent a primitive excr system which conspicuously differs from both mesonephros and nephros. According to Balfour's ('75) earlier view the segmental d formed by the backward growth of a single anterior evagination, may be regarded as the representative of a mesonephric tubule. ('81) later interpreted the pronephros similarly to Fürbringer, bu still inclined to believe that each mesonephric tubule was "in a s way serially homologous with the primitive pronephros." It is difficult for me to reconcile the latter opinion with his view tha pronephros is a primitive excretory system derived from Plathelmi while the mesonephros is a secondary (new) development which do appear until the trunk becomes segmented. Moreover, this view festly ignores the metamerism which is exhibited by the pronephro appears to me therefore entirely unsatisfactory.

Sedgwick ('81) first distinctly stated the conclusion that the nephros and mesonephros are differentiations of a single ancestral This view, which was adopted by Renson ('83), does not seem to been generally accepted, although several authors, by describing they denominate a transitional region, seem to me implicitly to a an intimate connection between the two glands. Mihalkovics ('8 65, 66) denied that they are *wholly* homologous, on the ground th pronephric tubules are peritoneal evaginations, whereas those of the nephros are differentiated in the solid Wolffian blastema. Mihal does not explain *his* use of the term *complete* homology, and I been unable to satisfy myself in regard to the precise relations he supposed to exist between the two glands.

an Wijhe ('88^{a}, '89), Rückert ('88), Hoffmann ('89), and Wieder-
im ('90), have distinctly denied the serial homology of the pronephros
the mesonephros. The objections of these authors to the view which
ave adopted have been most clearly formulated by van Wijhe ('89,
509, 510), whose account I shall follow in my criticism of their
tion. First, "the pronephros arises before the appearance of the
t or the mesonephros, and is indeed the first part of the excretory
em that appears." This point of difference is, as I have stated, the
t conspicuous feature in which the two glands are unlike. It is, how-
, not a weighty argument against their serial homology. Secondly,
e pronephros arises as an (in Selachii segmented) evagination of the
atopleure; its cavity, which may be temporarily obliterated by the
iferation of the walls, is formed as an evagination of the body cavity
tacölom). The mesonephros, on the other hand, is not formed as an
ination, and it is constituted of somatopleure as well as of splanchno-
re." This analysis seems at first sight to establish a fundamental
rast between the pronephros and the mesonephros, and I admit fully
cogency of the argument in disproving a comparison of the nephro-
al and glomerular portions of a mesonephric tubule with the
rostomal canal of the pronephros. On the other hand, however, I
ld insist that a hitherto unnoticed homologue of the pronephric evagi-
ons is to be found in the *outward growth* of the primitive mesonephric
l to join the duct.[1] (See page 301.) It is in precisely this way that
ndency to a somatopleural evagination would of necessity manifest
f. Thirdly, "the duct always appears in continuity with the pro-
ros, but always discontinuous with the mesonephros, which only
ndarily fuses with it and empties into it." This circumstance, as I
already shown, is a direct consequence of the condition explained
er the first head, Fourthly, "the mesonephros possesses Malpighian
uscles; while the pronephros has none, the glomus of the latter not
g homodynamous with the glomeruli of the mesonephros because it
vascular tuft invaginated into the secondary body cavity (Meta-
n)." This contrast appears to me morphologically inaccurate, as I
ve I have adequately shown in the preceding discussion.

further objection, which van Wijhe does not mention in his enumera-
is the occurrence of rudimentary mesonephric tubules in the somites
h formerly gave rise to the pronephros. To prove this assertion, it

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[1] This is the only portion of the mesonephric tubule which can properly be called
agination; the entire tubule comprises the evagination plus the communicat-
anal.

is usually regarded adequate to show the existence in the
region of metameric diverticula proceeding from the body cavit
the overlying protovertebræ. These diverticula are the comm
canals, and it is undoubtedly true that from similar canals i
terior region mesonephric tubules are actually developed; b
mind, the occurrence of these diverticula in the pronephric reg
be brought forward as evidence of the existence of two sets of
tubules in these somites, until it can be shown that these re
the canal-like communication between protovertebræ and late
exhibit some indication of the characteristic nephridial diffe
i. e. grow outward and join the duct. This, I believe, has n
demonstrated. The existence of such a growth has, however
serted by several observers; but it seems to me compatible
view I have expressed of the relations between pronephros and
ros. Since the time of the investigations of Balfour and of S
Selachians, it has been a familiar fact, that, although at firs
mesonephric tubule occurs in each somite, the further comp
the gland is largely produced by the formation of new tubu
proceed from the region of the primary Malpighian capsule
development of more than one tubule in a somite became nor
ancestors of the Craniotes before the separation of pronephros
nephros took place, the development of such secondary tubu
pronephric region would at once be intelligible.

A more fundamental objection is contained in an ignored o
of Gasser ('82, p. 96) on Alytes, according to which a typical
developed in the body cavity of the mesonephric region, in addi
universally present glomeruli. Gasser's account is contained i
short note unaccompanied by figures; it has not been confirm
subsequent observer; nor have I been able to find such a st
either Rana or Amblystoma. I am therefore inclined to th
that Gasser may have mistaken for the glomus either the gern
or the fat-body, both of which are developed in this region, alth
explanation would contradict the statement of Gasser that the
ric glomus is a transitory organ. Be that as it may, I canno
further evidence accept his account as final.

Semon ('90) has recently asserted that the pronephros and
ros are built upon the same structural type. He was led to
clusion by a study of the excretory system in Ichthyophis.
already alluded to the condition of the pronephros in this fo
characterized by the possession of a completely closed pronep

r, from which a portion of the nephrostomes ("inner" nephrostomes) ierge. Each nephrostomal canal, however near the nephrostomal end, joined by a branch which communicates with the permanent body vity by means of an "outer" nephrostome. According to Semon, the onephric chamber, as well as the cavity of a mesonephric Malpighian osule, is a diverticulum of the cœlom; and the nephrostomal canal ich joins the glomerular portion of a mesonephric tubule with the dy cavity is represented by those canals of the pronephros which erge from the open body cavity. The mesonephros is to be regarded a "generation" of excretory tubules younger than the pronephros, l the latter may be conceived to have primitively extended throughout entire trunk. In many features Semon's view is similar to that ex- essed in the preceding pages. The point of difference which I would re emphasize is the different way in which the nephrostomal canal of the sonephros is explained. According to my opinion, *this canal is a rem- at of the communication between the protovertebral cavity and the secondary ly cavity, and is not represented in the tubular portion of the proneph-* . Semon, on the other hand, claims that it is the homologue of the ter series of nephrostomal canals in the pronephros of Ichthyophis. nsidering the relations of the glands in that form alone, this view ms well justified; but it neglects the significant relation which has ently been shown to exist between the mesonephros and the com- nicating canal; and I am of opinion that the view as applied to other rtebrates is untenable, unless it can be shown that the outer nephro- mal tubule of the Gymnophionian pronephros also develops from that ial. The latter interpretation is, I must admit, at least possible; we must await further researches on the development of these aphibia before accepting such a conclusion.

The closing section of this discussion will be devoted to a consider- on of the evidence which the development of the excretory system as vhole throws on the origin of Vertebrates.

Two methods of investigation, which are mutually dependent, yet te unlike in their application, may be employed in attempting to w phylogenetic conclusions. One of these methods is peculiar to bryological research; it is dependent upon the principle that on- geny is in part an abbreviated recapitulation of phylogeny; its thod is to eliminate cœnogenetic characters; it accomplishes this gely by the aid of a physiological estimate of the influences of lar- and embryonic environment, and it is comparative only throughout the extent of the group whose origin is sought. The other method is common both to comparative embryology and to comparative anatomy; it is dependent upon the inherent improbability of the same physiological requirements, being met by the same structural device in two groups which are not genetically related; it can employ equally well, though with a somewhat different significance, both cœnogenetic and palingenetic characters; it is purely anatomical in its method, and it is in the broadest sense comparative. The first I may designate as the method of elimination, or the intensive method; the latter as the comparative, or extensive method.

I have been led to make the preceding analysis in order to employ the division thus indicated in the subsequent discussion, and also because it is a contrast which does not appear to be generally recognized. Thus, a recent text-book of zoölogy (Hatschek, '88, pp. 25, 26) identifies the methods of embryology with those of comparative anatomy, and declares that palingenetic and cœnogenetic characters are equally valuable for phylogenetic inferences. According to the preceding analysis, these two statements are partial, relating only to the comparative method in embryology, and ignore the higher use which renders embryological facts of peculiar value.

Observing then this two-fold division in the following discussion, an attempt will first be made to reconstruct from the ontogeny of Vertebrates the ancestral history of their excretory organs.

The most general character which appears to be common to the ontogeny of all Vertebrates is the intimate relation which exists between the excretory tubules and the cœlom. This relation is peculiarly well illustrated by the pronephros, but it is true also of all the urogenital organs, and is a fact which in my opinion throws considerable light on their evolution. The cœlom appears to be an internal cavity developed to meet a number of physiological needs. It is likely that in the lower Invertebrates the cœlom served largely a nutritive function (see, e. g., Chun, '80, pp. 248–253); but I am of opinion that in the higher Invertebrates and in Vertebrates the cœlom early became in large measure an excretory space. This function of the cœlom, inferred from its relations with nephridia, is in accord with its situation in the body. Evidently the organs which would be most in need of a near place of discharge for nitrogenous waste products are those which are in the highest degree metabolic. Such are, *par excellence*, the muscle masses of the body, and it is a familiar circumstance that in all Chordates the primitive muscle plates develop from the lining wall of the dorsal segmented por-

n of the cœlom. It is very probable that this arrangement represents
earliest differentiation of a special excretory surface of which evi-
nce is preserved in the ontogeny of Vertebrates.

The next step in the specialization of the urinary organs is the es-
lishment of definite conduits for the purpose of conveying the excreted
ducts to the outside. It is possible that simple apertures, such as
abdominal pores, at first served this end; or, if the enterocœlous
dition represent a phylogenetic stage, communications with the
stinal tube may have afforded an outlet to the excreted fluids. Be
as it may, it is evident that the ancestors of our present Vertebrates
ly acquired specialized tubes subserving this purpose.

n the account of the development of the Amphibian pronephros and
t given in the first section of the present paper, emphasis was laid
n the fact that these structures are differentiated from a solid so-
topleural thickening, and do not arise as a fold of the peritoneum.
nifestly the former condition is cœnogenetic; such a solid thickening
ld in no wise function as an excretory conduit. On the other hand,
must not be rashly assumed that the somatopleural thickening is a
guised *fold* of that layer. On the contrary, the pronephros, on canal-
ion, shows itself to be already composed of a series of metameric
ginations of the cœlom, and it is perfectly conceivable that the pro-
hric thickening is a modification from a condition where the separate
ginations had their *independent* means of communication with the
erior, the several diverticula being fused into a solid mass. Either
rpretation would be physiologically intelligible. In the first case, a
ain region of the peritoneum would first sink as a groove into the
etes of the cœlom. This channel might, like the nephrostomes, be
vided with vibratile cilia, and might thus serve to carry the fluids
ged in it back to a single pair of orifices situated near the posterior
of the cœlom. As a further differentiation, it is to be conceived
t this groove became at intervals constricted off from the cœlom,
ning a retroperitoneal duct with a series of nephrostomal tubules.

ccording to the second alternative, it is necessary to suppose that
several evaginations communicated distally either directly with the
erior or with an independent longitudinal duct. The nephridia of
eromastus and Capitella (Eisig, '88, pp. 242, 272), in which no ex-
nal opening is present, show us that the gradational steps in the
nation of such outgrowths may be conceived to be functional.

n judging between the two views to which allusion has just been
de, it is important to consider whether the ontogeny of other groups

ever presents either of these processes in an unambiguous manne
have already expressed my doubts in regard to the development c
pronephros and duct by the incomplete closure of a groove of so
pleure. The best attested claim that has been made for such a
of origin was that made by Goette, Fürbringer, Hoffmann, and Ma
and Bles, for Amphibia; but this position is distinctly contradicte
my own observations. Indeed, this mode of origin has been rec
denied in the case of every class except Teleosts, a group in which
very difficult to obtain accurate evidence respecting the early histo
the mesoderm.

On the other hand, numerous recent investigators have describe
first rudiment of the pronephros as a series of distinct evagina
Such observations have been recorded in Cyclostomes by Kupffer (
in Ganoids by Beard ('89), and in Amniotes by almost all write
their early development. It seems to me, therefore, that the mo
formation by means of serial evaginations has a far wider distribu
and is more clearly attested, than that by means of an incompl
closed fold. I am of opinion that the condition in Amphibia and
chia is to be regarded as derived from such evaginations by mea
cœnogenetic modification; and that the weight of internal evidence
favor of the view that the tubules were primitively distinct.

Typically the nephridial tubes are strictly metameric, one pa
tubules being developed in each metamere. The occurrence of se
nephridia in a somite occurs, as we have seen, in the case of the
nephros of certain Amphibia. This condition seems to me to be a
acter secondarily acquired. The following reasons confirm this opi
(1.) In other forms, the strict metamerism of the nephridia is th
liest ontogenetic condition, the duplication of the tubules appearing
later. (2.) The dysmetameric arrangement seems to be correlated
the limited number of somites which are, in such cases, involved i
formation of the mesonephros; thus, in the Anura, a group in whic
number of trunk somites is extremely small, the mesonephros de
most widely from the metameric condition; in Urodeles, the numb
somites is larger, and there is an indication of metamerism in the an
tubules; and again in Cœcilia, where the number of somites is stil
ger, the mesonephros has the typical metameric arrangement. (3.)
pronephros, which in general represents the least modified portion c
excretory system, retains a metameric condition in those forms in
this arrangement is absent in the mesonephros.

In order to ascertain the probable mode in which the metameric c

la primitively terminated, whether they opened on the surface or
ed a longitudinal duct, it will be necessary to consider the pronephros
ne, since the segmental duct is already present before the mesonephros
ormed, and we cannot expect to find an adequate criterion for deter-
ing whether the union of the mesonephric tubes with the duct be
nitive or secondary. In the pronephros there is in most cases no
lence of a mode of termination more primitive than that of com-
nicating with a duct. Two arguments, however, occur to me, which
n to indicate that a series of direct outlets to the exterior may have
n early present. In the first place, the pronephric diverticula have
uently been observed to enter into intimate union with the ectoderm.
is Rückert ('88, p. 217) was led to believe that the pronephric thick-
ng of Selachians even received a contribution of cells from the outer
n layer. The most natural explanation of this condition seems to me
be, that the fusion of the diverticula with the ectoderm is the re-
itulation in the ontogeny of a phylogenetic stage, which possessed
hridia provided with direct openings to the exterior. Secondly,
phioxus, according to the most recent investigations, is provided with
eries of nephridia opening into the atrial chamber, which latter we
in my opinion, justified in regarding as a simple infolded portion of
exterior. Accepting the homology of the nephridia of Amphioxus
those of Craniotes, it seems to me probable that the ancestors of
tebrates possessed nephridia which resembled those of Amphioxus in
ning directly to the exterior.

f separate diverticula leading from the cœlom to the exterior be the
nitive condition of the Vertebrate excretory organs, we have still to
k the origin of the segmental duct. On this point, the pronephros
ne can afford evidence. The participation of the ectoderm maintained
many authors for the posterior end of the duct affords the suggestion
t it may have first been formed as a groove of that layer, or that a
nitive anterior opening was gradually shifted back to the cloaca. It
y be objected to this view, (1) that in many Vertebrates no participa-
n of the ectoderm occurs, while in none has it been shown that the
soderm does not play a part in the formation of both anterior and
terior portions of the duct; and (2) that the longitudinal canal of the
nephros, which forms the anterior prolongation of the duct, in no case
es in this way. In the pronephros the longitudinal canal arises, as
tified by a large number of recent investigators for divers groups, and
confirmed by my own observations on Amphibia, by the fusion of the
tal ends of the pronephric diverticula. This mode of development

seems to me entirely in harmony with physiological requirements in this earliest fragment of the excretory system we have, in my op a remnant of the primitive mode of formation of the segmental duc

The question at once arises whether there is any indication o mode of origin preserved in the development of the posterior porti the duct. A free backward growth, such as is maintained for Vertebrates, is evidently far removed from the primitive mode of f tion, and is to be regarded as an adaptation to the needs of the pro ros. The origin of the duct *in situ* from a somatopleural prolife is without doubt a modified condition ; yet it suggests a mode of which is in agreement with that observed in the anterior region. I already emphasized the circumstance that in Amphibia the duct from a mass of cells which is perfectly continuous with that from the pronephric tubules are differentiated ; and it is possible that regions represent disguised nephridial evaginations of which those i posterior region are never differentiated as actual canals except in portions as are converted into the duct. Further evidence in fav this view is afforded by the occasional occurrence of supernumerar nephric tubules such as have been observed by Mollier ('90, p. 224 myself (page 253). The acceptance of this interpretation would ne tate a modification of our conception of the relations between prone and mesonephros, since we should be obliged to regard the meson tubules as a second generation of tubules, the first generation h been employed in giving rise to the duct. On the other hand, it is possible that the entire backward growth of the duct is a *wholly* dary process to meet the needs of a prematurely developed portion primitive excretory organ. This is the only interpretation which admissible in those cases where the duct has been found to grow ward free from adjacent tissue.

The conception of the phylogeny of the duct which I have jus sented offers a partial explanation of the contradictory evidence has been advanced respecting the germ layer from which the duct With a narrower conception of the phylogeny of the duct, it is dif to understand why the ectoderm should participate in the formati the excretory system in one group, but not in another, and why posterior end of the duct should in some cases be formed at the ex of a germinal layer different from that which gives rise to its an portion and to the nephrostomal canals wherever they appear. If, ever, we assume the existence of a phylogenetic stage in which a of nephridia open directly to the exterior, it is at once evident t

trifling difference of location would determine whether the longi-
nal canal, by means of which the duct arises, should develop from
nesoderm or from the ectoderm. It is to be remarked, however,
such an explanation is not wholly satisfactory, since one would
ct on this hypothesis that those forms in which the ectodermal
n of the duct seems well attested would show evidence of close
tic relationship, while those classes in which the duct arises from
mesoderm ought to form an equally well defined group. This
ition, however, is by no means realized. On the other hand, the
of this objection is materially weakened if we regard the duct as a
nt acquisition, which its absence in Amphioxus gives some justifica-
for assuming. The explanation seems to me, nevertheless, in a
ure unsatisfactory, and I have adduced it merely as a possible solu-
of the problem to which the apparently diverse relations of the duct
e germ layers gives rise.

n intimate relation is always very early established between the
tory tubules and the cardinal veins. Such an arrangement is so
able for the process of secretion that there can be but little doubt
this condition prevailed in the ancestors of all Vertebrates. There
not appear to be any evidence which would indicate whether the
nal veins or the excretory tubules are the more primitive structures.

addition to the means of excretion afforded by the epithelial walls
e tubules, the Vertebrate kidney-organs possess peculiar glomerular
tures. These, as I have already shown, are all formed on the type
e pronephric glomus. In their primitive condition, they consist of
lar tufts, which receive blood from the aorta and project into the
cavity from the root of the mesentery.[1] The origin of such a prim-
glomerular structure is not far to seek. It is readily conceivable
fluid may at first have simply exuded from the aorta, and, travers-
he small amount of tissue intervening between it and the body
y, may have reached the orifices of the excretory tubes prior to
levelopment of any specialized organ subserving a glomerular func-
This process being once established, any modification of structure
h should allow a portion of the aortic current to be brought into
r relations with the excretory tubules would be of obvious utility,
would be preserved.

e excretory system thus constituted would represent the proneph-

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[1] The view of the excretory system here presented explains the double blood
y of the kidneys of lower Vertebrates, and also the circumstance that the
ighian bodies always receive their blood by a direct branch from the aorta.

ric type of structure. I have already sketched the manner in v
the mesonephros may be derived from the pronephros by supp
the metameric segmentation of the body to extend to that portion c
cœlom from which the nephrostomes emerge. The account given i
preceding section of this paper regarded the tubules as passive in su
metamorphosis. It is possible, however, that the transference o
tubules to a segmented portion of the cœlom may have been in
effected by a dorsalward shifting of the nephrostomes. In either
I am of opinion that the mode of development which I have now
gested is applicable alike to the pronephros and the mesonephros, a
may also add to the metanephros (see Sedgwick, '80).

I have now presented, in a suggestive manner rather than as a
plete argument, certain indications of the phylogeny of the excr
system which may be obtained from internal evidence. It still rem
for us to consider what conclusions are justified by a comparative s
of the excretory system, and whether the phylogenetic stages sugg
in the foregoing account are to be found in any group of living anim

The sole purpose of this discussion is to ascertain the most pro
phylogenetic line of development for the excretory system of Verteb
For this reason, I shall avoid any discussion, which would necessar
lengthy, respecting the interrelationships of the diverse excretory o
found in Invertebrates, simply endeavoring to seek out those c
which possess nephridia similar to those of Vertebrates, and shall i
the further consequences which would follow from the assumption
homology in any single case.

In the preceding account, I have provisionally accepted the
that Amphioxus belongs to the Vertebrate phylum, and have en
ored to interpret its kidneys in accordance with that view.
Tunicates it is quite different; not merely do they afford no assis
in the solution of the problem in hand, but it has hitherto prove
possible to find any organs in this group which can be regard
homologous to Vertebrate nephridia.[1] In my opinion, it cann
objected that the absence of such organs in Tunicates proves tha
Vertebrate nephridia arose within the Vertebrate phylum. A rigi
herence to such a system of restriction in the case of other organs v
quickly lead to absurd conclusions.

The only classes of animals in which we need seek for a homolo

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[1] Hatschek ('84, p. 519) regarded the single nephridium described by I
Amphioxus homologous with the neural gland of Tunicates; but I have a
pointed out the probable inaccuracy of this observation.

Vertebrate renal organs are those belonging to the bilateral cladus ; among these I shall consider only those forms which are usually uded in the rather heterogeneous class Vermes. This restriction is ified by the circumstance that the only similarities of structure ch are to be found between the excretory system of Vertebrates and se of Mollusks and Arthropods recur with greater force in the case of eral groups of Vermes.

n comparing the kidneys of Vertebrates and those of Worms, I shall inguish three types of structure in the latter group : (1) the water- cular system of Plathelminthes, (2) the excretory system of Nemer- s, and (3) the nephridia of Annelids. The various organs which ve as excretory and genital passages in Rotifers, Nematodes, Echi- ls, and Sipunculids are either referable to one of these types, or are eless for the purpose in hand.

n endeavoring to find what points of similarity exist between the retory system of Plathelminthes and that of Vertebrates, I have been ble to formulate any more definite statement than that both consist ongitudinal internal canals, which bear numerous lateral branches, which open directly or indirectly to the exterior. On the contrary, two sets of organs appear to me to perform the function of excretion anatomical devices which are diametrically opposed. In Vertebrates, excretions are either (primitively) poured into the cœlom and con- ed thence by a simple series of conduits, or excreted from the blood he course of the tubuli uriniferi of the kidneys. In Plathelminthes, the other hand, the excretory tubes ramify throughout the entire y parenchyme, and, so to speak, seek out the waste products of abolism at the seat of their formation. It is a contrast such as ts between lungs and tracheæ, and appears to me of fundamental ortance. According to Fraipont ('80) and Francotte ('81 and '83, 734, 735), it is true, there is a communication between the excretory ules of Plathelminthes and certain interior canalicular spaces, which y interpret as a rudimentary cœlom. The evidence in favor of the er interpretation is certainly far from complete, but could not, if e, overthrow the fundamental contrast which I have just emphasized. thermore, I am not aware that any subsequent writers have con- ned this account of the termination of the excretory capillaries ; while tner ('80, p. 302), von Graff ('82^a, pp. 106 *et seq.*, '82^b, p. 80), Lang l, p. 208, '84, p. 167), Iijima ('84, p. 400), Zschokke ('87, p. 165), l Böhmig ('90, p. 243) have all asserted that the terminal sacs are irely closed. The conclusion seems warranted that no direct evidence in support of an intimate relation between Vertebrates and P helminthes is afforded by a comparison of their excretory organs.

In Nemertines the excretory system is in peculiar relations with blood vascular system. According to Oudemans ('85), the excret system of the Schizonemertini and the Hoplomertini consists of a lo tudinal tube, which is closely applied to the lateral longitudinal blo vessel of the œsophageal region, and this tube communicates with exterior by means of a single excretory pore or by a number of s openings. In Carinella and Carinoma, however, the connection is m more intimate, and the glandular portion of the excretory organ embedded in the œsophageal blood lacunæ and communicates with latter by means of two or three evident openings. Oudemans asse indeed, that the excretory system is in reality a detached portion of blood vascular system. Bürger ('90, p. 92), however, has recer thrown some doubt upon the existence of open communications betw the nephridia and the blood-vessels, but reaffirms the close depende of the excretory system upon the vascular trunks.

Comparing the nephridia of Nemertines with those of Vertebrate seems to me that one cannot fail to recognize a pronounced differenc type. In Vertebrates the nephridia are canals in close relation with cœlom; they develop from its epithelium, and even in the adult s from chambers which must be regarded as detached portions of cœlom. The excretory organs of Nemertines lie between the vasc trunks and the exterior, and show no such relations with the cœlom.

Among the Annelids, on the other hand, the Chætopods posses excretory system which seems to present several features of str resemblance with the nephridia of Vertebrates, and it remains to considered whether an actual homology can be postulated in this case

The points of similarity may for the present purpose be classed un seven heads. (1.) The Vertebrate and the Chætopod excretory syst agree in the fact that both primitively serve, at least in part, to conve the exterior such fluids as accumulate in the cœlom, this cavity being as a capacious excretory reservoir. (2.) In both groups certain port of the epithelial lining of the cœlom become differentiated into special excretory glands. In Vertebrates the only structures of this character the glomi and glomeruli; but in Annelids there is evidence that siderable areas of the peritoneum may become modified in this way. was suggested by Claparède ('69, p. 615), that the chloragogen secrete certain elements from the blood and transfer them to the visceral fluid. This view of the function of the chloragogen cells n confirmed by a large number of observers,[1] and it has been further wn that individual cells, having become charged with excreted connents, loosen from the layer to which they belong, and float freely in cœlom, whence they are discharged through the nephridia. The ragogen layer covering the blood-vessels appears moreover from its omical relations to be a portion of the visceral mesoderm, and it been shown to arise ontogenetically from that layer (Roule, '89, 201, 252, 290). The chloragogen cells are frequently distributed n special vascular processes, thus forming distinct glandular organs. ilar in function is probably the glandular envelope of the ventral el in Polyophthalamus (E. Meyer, '82, p. 816), and cases may be d among Polychætes in which definite peritoneal glands are present bben, '88, pp. 255 *et seq.*, Eisig, '87, pp. 227, 245, 681). I should not to assert a strict homology between the glomus and the masses of ragogen cells ; yet it seems to me likely that the latter represent an differentiation of the splanchnic mesoderm of which we have more ialized developments both in Annelids and in Vertebrates.[2] (3.) The ent conduits take their origin from the cœlom by means of a series liated funnel-shaped openings, the nephrostomes. (4.) The nephroes lead into transverse convoluted canals, along the course of which a part of the excretion takes place. (5.) The nephridial tubes arise the parietal peritoneum. (6.) They are typically strictly metaic, one pair of tubules being developed in each metamere. The ation from this typical metamerism to which I have already referred e case of Vertebrates is paralleled by similar conditions in Capitella ig, '87, p. 594). (7.) The development of the Chætopod nephridia mbles in general that shown by those of Vertebrates. Both the ephric and mesonephric tubules arise as a series of metameric rowths from the somatic mesoderm. In Polychætes this is evidently mode of origin of the nephridia. In Oligochætes the development is doubtful, but the method of origin described by Bergh ('90) is in nce the same as that known in Polychætes, and the mode of develent maintained by Wilson ('87, pp. 185, 186, and '89, pp. 419 *et seq.*) be interpreted so as not to be in fundamental opposition with such thod.

here is one feature in regard to which the nephridia of most Anne-

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[1] E. g. Timm ('83, pp. 122, 123); Kükenthal ('85, p. 336); Meyer ('87, p. 648).

[2] A further analogy is possibly to be found in the fact that in Amphibia certain early loosen from the wall of glomus and fall into the cœlom, leaving interbetween the remaining cells of the epithelium.

lids and those of Vertebrates differ conspicuously, viz. in the mod
which the nephridia terminate. It is a familiar fact, that in Anne
each nephridium opens separately on the surface of the body; whil
Vertebrates the nephrostomal tubules all connect with a pair of lo
tudinal ducts opening into the cloaca. In commenting upon this
ture of difference, it is important to note in the first place that
contrast is not of universal application. It has been recently show
E. Meyer ('87, pp. 618–625) and Cunningham ('87^{a}, 87^{b}, pp. 248–
that in Lanice conchilega, a terebelloid Annelid, certain nephridia
into a longitudinal trunk, and only secondarily communicate with
exterior. On the other hand, it is probable that Amphioxus posse
nephridia which open to the exterior (atria cavity) without the in
vention of a longitudinal duct. If such differences can occur among
members of either group, it seems to me that it would be unjust to d
the homology of the other portions of the system in consequenc
the fact that Vertebrates *in general* possess a longitudinal duct, w
Annelids *in general* do not. It appears to me, moreover, that the
dition of the nephridia in Lanice conchilega and the ontogeny of Ve
brates both serve to indicate the manner in which the duct may
secondarily arisen. In Lanice conchilega there is no doubt that
nephridial duct is a secondary growth, and it is highly probable that
channel is formed by outgrowths extending from each of the nephri
tubes backward and communicating with the next following neph
ium. Two groups of nephridia can be distinguished in Lanice
chilega. The more anterior of these consists of a short longitudinal
which bears three nephrostomal tubules, and terminates at its poste
end by a single pore. In the posterior set, the longitudinal duc
merely a canal which connects the several nephridia, while these
tinue to retain their external orifices. I have already pointed
that the ontogeny of Vertebrates presents a similar process in the de
opment of the longitudinal canal of the pronephros, and have sh
that such changes may likewise have taken place in the region of
mesonephros. I by no means wish to imply by this comparison a b
that the ordinary mode of development in Vertebrates is to be dire
derived from that presented by Lanice conchilega, nor to assume a c
genetic relation between Vertebrates and genera presenting this co
tion. I merely wished to emphasize the fact, that in Lanice conchi
we have an instance of a species which, primitively possessing disc
nephridia, such as may have been present in the ancestor of Vertebr
has acquired a longitudinal excretory canal by a process of transfo

n which resembles that by which Vertebrates acquire in their ontogeny e segmental duct.

From the facts thus far brought forward, I conclude, (1) that the oup of animals which presents nephridia most closely resembling those Vertebrates is unquestionably that of the Chætopod Annelids; and) that the Vertebrate excretory system can be readily derived from at of Annelids by a series of steps which are in accord with the evi- nce afforded by the ontogeny of Vertebrates.

In conclusion, I shall briefly allude to the opinions of previous writers pecting the origin of the Vertebrate excretory organs. These opin- s fall, in the first place, into two classes, according to one of which the cretory system is derived from Invertebrate ancestors; according to other, it has arisen wholly within the Vertebrate phylum.

The most recent exponent of the latter view is van Wijhe ('89, pp. 6 *et seq.*). The arguments offered by this author in support of his ition are in part dependent upon his denial of the serial homology of nephros and mesonephros. Van Wijhe also employs two arguments ich are independent of his position in regard to this point: (1) ne- idia are absent in Amphioxus, and therefore the common ancestral m cannot have possessed them; (2) the renal organs do not appear il after the so-called "Acrania stage," and therefore could not have eared phylogenetically until this stage had been passed. Granting h premises, it seems to me that neither conclusion follows. With erence to the absence of kidneys in Amphioxus, the possibility — or uld I not say probability? — of extensive degenerative modification is irely neglected. Moreover, it has now been rendered probable that e nephridia do exist in Amphioxus, an observation which removes at low the whole basis of the argument. I do not believe many embry- gists would unite with van Wijhe in holding that characters which ear simultaneously in the ontogeny of a form must necessarily have en contemporaneously in its ontogeny. For my part, I am unable to gnose with accuracy the "Acrania stage" of Amphibia; but Ostrou- ff ('88, pp. 77, 78) appears to have had the necessary insight, and ies emphatically that the pronephros in the case of Reptiles arises r the "Acrania stage."

Turning now to the hypotheses that have been advanced involving derivation of the Vertebrate excretory system from Invertebrate an- tors, Haeckel ('74, p. 37), Gegenbaur ('78, p. 628), and Fürbringer 8^{a}, pp. 95 *et seq.*) endeavored to show that the Vertebrate nephridia e derived from those of Plathelminthes. Semper and Balfour, on the other hand, claimed that the transverse tubules of the mesonephros ar homologous with the segmental tubes of Annelids, an opinion which i shared by Beard, Haddon, Kollmann ('82^{a}) and others.

Rückert ('88, p. 262) has recently denied this homology, and asserte that the Annelidan nephridia are represented in the pronephros alon since the latter is the only portion of the system of metameric tube which comes in contact with the ectoderm. With Rückert, I woul admit that the evidences of an Annelidan origin of the excretory syste are to be sought mainly in the pronephros; but, in view of the intimat relations which exist between pronephros and mesonephros, it seems t me more probable that both have had the same phylogenetic origi Ostroumoff ('88, pp. 80 *et seq.*) also has asserted that the development c the pronephros indicated that this system had been inherited fro Annelidan ancestors.

On the other hand, a number of authors maintain that, although th mesonephros may be derived from the segmental organs of Annelid the pronephric system is represented by other Invertebrate nephridi Thus, Semper ('76, pp. 387, 388) suggests the possibility that the duc (pronephric system so far as present in Selachians [1]) may represent th unsegmented excretory tubules developed in the larva of Nephelis, c may even represent an inheritance from the Plathelminthan water-va cular system; and Balfour ('81, p. 607) was led to accept this view.

In addition to his hypothesis of an origin of the excretory system c Vertebrates from that of Plathelminthes, Fürbringer suggests the possi bility that the entire system may have arisen from Gephyreans, in whic unsegmented and segmented excretory organs are stated to coexist. Thi view was adopted by Kollmann ('82^{a}), and is offered as a suggestion i Wiedersheim's ('86, p. 731) text-book.

None of the views which claim a *double* origin for the excretory syster seem to me to be tenable, in consequence of the fact that the pronephro an undoubtedly segmented element, develops in *strict continuity* wit the duct, the so-called unsegmented element. The view according t which the excretory system is derived from that of Gephyreans, mor over, is liable to special criticism. This claim that Gephyreans presen an excretory system of a double nature, segmented and unsegmente doubtless refers to the coexistence of two or three pairs of nephridi together with the so-called Analschläuche of Echiurids. I am unable t see the slightest evidence that the Vertebrate excretory system is mad of such remote parts; and the hypothesis must fall to the ground as n as it is proved that the Analschläuche are in reality only modified hridia opening into a proctodæum. In addition to the anatomical lence favoring such an interpretation, Hatschek ('80, pp. 60–62) has ntly advanced strong evidence from an embryological standpoint for eving that they are nephridia which primitively opened directly to exterior.

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[1] By this suggestion, Semper allows some justification to W. Müller's conceptio of a pronephros, although he had earlier contested it.

mong the attempts to find a homologue of the segmental duct already ent in the Worms may be mentioned the longitudinal canal described Hatschek ('78, p. 117 *seq.*) in the larva of Polygordius. Were Hatek's account accurate, it would doubtless warrant great changes in conceptions of the interrelationships of the Vermian nephridia, and of origin of the Vertebrate kidneys; but his statements have not been firmed by any subsequent observations, though several investigators e concerned themselves with this interesting form (Fraipont, '87, 3; Eisig, '87, p. 662; E. Meyer, '87, p. 594; Bergh, '85, p. 27, foot-).

he remaining views in respect to the nature of the duct agree in reding it as a secondary growth.[1] Beard ('87, p. 651) and Haddon) accept the ectodermal origin of the segmental duct, and endeavor give it phylogenetic significance by assuming that the ontogenetic nection of the duct with the ectoderm indicates that it was repreed in the phylogeny at first by a groove into which the nephridia ned, and that this groove gradually became closed and was cut off tube extending from the most anterior tubule backwards to the ca. Rückert ('88) and van Wijhe ('89, pp. 507, 508), on the r hand, assert a gradual backward growth of a primitively anterior ning.

one of these views are compatible with the fact that in many Vertees the duct is demonstrably of mesodermal origin. They also seem ne to give insufficient significance to the mode in which the pronephric rticula unite to form a longitudinal canal; and the first two authors ect it wholly.

inally, the abandoned view of Balfour ('76, pp. 25, 26), according to ch *the duct arises by the fusion of the distal ends of the several nephridia,* been revived by Eisig ('87, p. 649), and was accepted by Rückert , p. 264) for the *pronephric portion* of the duct. This view seems to much the most probable, and I am inclined to accept it.

Here belongs also the view of Boveri ('90), which has already been discussed e 265).

In the foregoing discussion, I have endeavored to sho considerable evidence in favor of the view that the excre Vertebrates has developed from a system of metameric as are present in Annelids. None of the evidence seen ever, final. The excretory systems of the two groups a but we have no means of limiting definitely the part played by physiologically similar needs in moulding the s organs. Nor am I committed to the theory of the Annel of Vertebrates. I fully realize that such a theory can lished by investigations which shall include in their scop ganization of the two groups. So far as this larger t dealt with in this discussion, it has been with the view such evidence as the excretory system offers, and I hav untouched the mass of evidence which proceeds from oth this in addition we must appeal for the justification theory.

CAMBRIDGE, April 25, 1891.

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EXPLANATION OF FIGURES.

the Figures, unless otherwise stated, were drawn with the aid of an Abbé ra lucida, and represent the appearance of the *anterior* faces of the sections. s I.–IV. were made from preparations of Rana sylvatica Le Conte; Plates III. from Rana sylvatica Le Conte, Bufo americanus Le Conte, and Ambly- punctatum Linn.

ABBREVIATIONS.

(For the meaning of letters *a*, *b*, *c*, *d*, *e*, *f*, in Figures 24–26, see t
of those Figures.)

ao.	Aorta.
can. comn.	Communicating canal.
cd. spi.	Spinal cord.
cl. ms'drm.	Mesodermal cells.
cl. vt.	Yolk cells.
clc.	Cloaca.
cœl.	Cœlom.
cœl.'	Protovertebral cavity.
cœl.''	Body cavity.
cp. sng.	Blood cells.
cps. pr'nph.	Pronephric capsule.
cras. gn.	Ganglionic thickening.
cras. pr'nph.	Pronephric thickening.
cras. so'plu.	Somatopleural thickening.
d.	Dorsal aspect.
dt. sg.	Segmental duct.
dt. Cuv.	Ductus Cuvieri.
dx.	Right side.
ec'drm.	Ectoderm.
ec'drm.'	Superficial layer of same.
ec'drm.''	Deep layer of ectoderm.
en'th.	Endothelium.
fnd. arc. vr.	Deep layer of a vertebral arch.
fnd. cps.	Fundament of the pronephric capsule.
fnd. dt. sg.	Fundament of the segmental duct.
fnd. glm.	Fundament of the glomus.
fnd. glm.'	Fundament of glomerulus.
fnd. gn. spi.	Fundament of a spinal ganglion.
fnd. mbm.	Limb bud.
fnd. ms'nph.	Fundaments of mesonephric tubules.
fnd. nph'st.^{I}	Fundament of first pronephric nephrostome.
fnd. pul.	Lung bud.
glm.	Glomus.

gn. nd.	Ganglion n
gn. spi.	Spinal gan
hp.	Liver.
in.	Intestine.
la. l.	Lateral pla
la. med.	Medullary
la. ms'drm.	Mesoderma
la. pi'ton.	Peritoneal
la. pr'vr.	Protoverte
la. so.	Somatic la
la. spl.	Splanchnic
m.	Median.
mb. ba.	Basement
ms'drm.	Mesoderm.
ms'chy.	Mesenchyn
my'tm.	Myotome.
n. l.	Nervus lat
n'cd.	Chorda do
nph'stm.	Nephrosto
nph'stm.$^{I., II., III.}$	1st, 2d, nephrost
pi'ton.	Peritoneun
pr'vr.	Protoverte
rx. ao.	Aortic roo
rx. vag.	Root of th
sb.-n'cd.	Sub-notoch
sn. sng.	Blood sinu
so.$^{I., II.,}$ etc.	Somites I.,
so'plu.	Somatople
sph. vt.	Yolk spher
spl'plu.	Splanchno
tbl. nph'stm.$^{I., II., III.}$	1st, stomal tub
tbl. pr'nph.	Pronephric
trn. clg.	Collecting
trn. com.	Common t
va. sng.	Blood-vess
vn. crd.	Posterior c
vn. jgl.	Jugular vei

343

PLATE I.

Fig. 1. A portion of a cross section through the anterior trunk region of one of the older embryos included under Stage I. × 110.

" 2. A cross section through the same embryo in the middle trunk region. × 25.

" 3. A portion of a cross section through the middle trunk region of one of the younger embryos in Stage I. × 92.

" 4. A portion of a cross section through the hinder trunk region of one of the younger embryos belonging to Stage II. × 92.

" 5. A portion of a cross section through the anterior trunk region of one of the older embryos from Stage II. The section passes through an interprotovertebral septum. × 110.

" 6. A portion of a cross section from one of the older embryos in Stage III. The plane of the section passes through the middle of Somite III. × 110.

" 7. A small segment of a cross section through the embryo shown in Figures 15–17 of Plate II. The Figure represents a portion of the ventro-lateral ectoderm with three subjacent mesodermal cells. × 615.

" 8. A portion of a cross section through the embryo shown in Figures 18–22, Plate III. It shows the fundament of the glomus. × 110.

" 9. A portion of a cross section through a slightly older embryo, showing the glomus in a more advanced stage of development. × 110.

" 10. A portion of a cross section through an embryo of Stage V., showing a branch of the aorta which gives off a small vessel to the glomus. × 150.

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10.
sn.sng.
npl.stm
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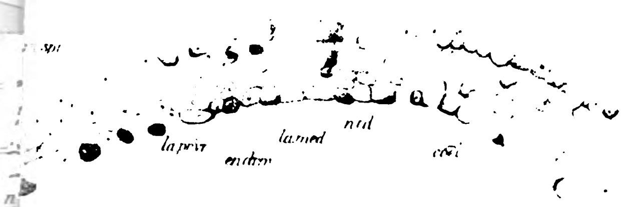
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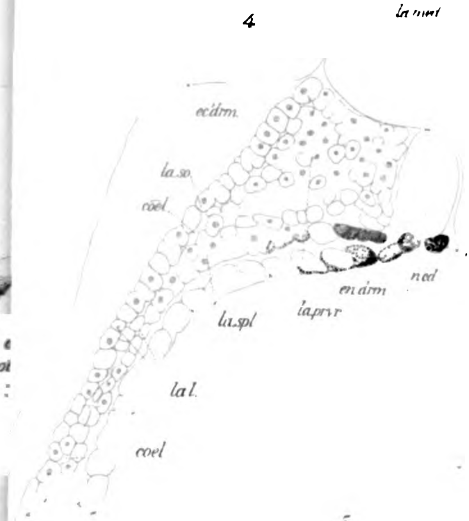
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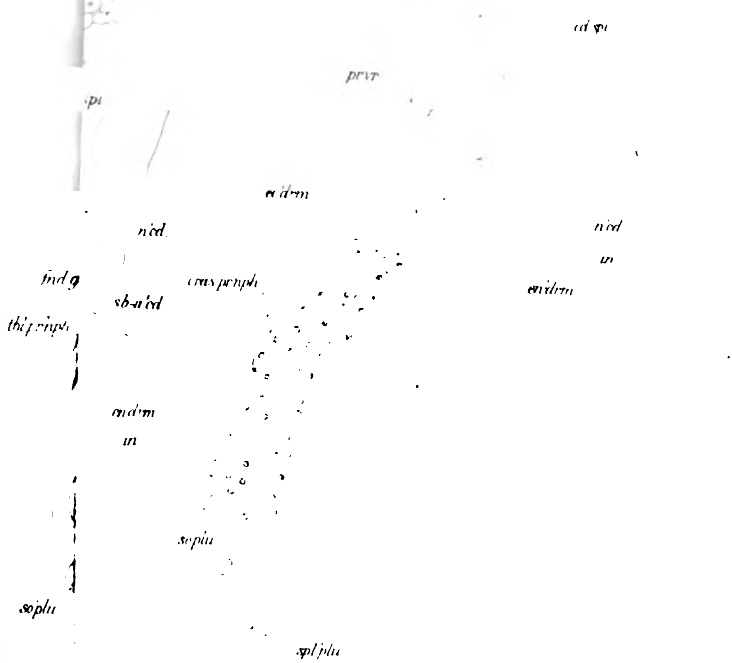
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PLATE II.

All the Figures on this plate are magnified 110 diam

Figs 11 and 12. Portions of two frontal sections through the pr
ing of one of the older embryos belonging to Stage

Fig. 11 shows the dorsal margin of the thickening.

Fig. 12 shows a section through the nephrostomal region.

Figs. 13 and 14. Portions of two frontal sections from one of the
of Stage II.

Fig. 13 shows the ventral ends of the anterior protovertebræ.

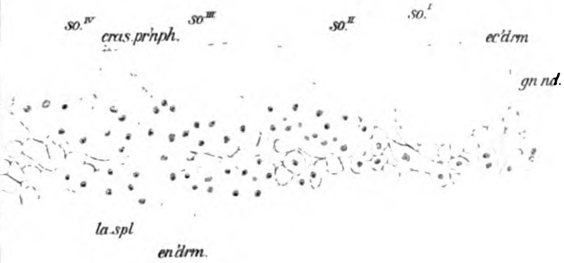
Fig. 14 shows a section through the dorsal portion of the proneph

Figs. 15–17. Portions of three cross sections through one of the
of Stage III.

Fig. 15 shows the anterior end of the pronephric thickening.
section passes a little behind the middle of Somite

Fig. 16 shows the pronephric thickening in the region of Somite

Fig. 17 shows the thickening near its posterior termination.



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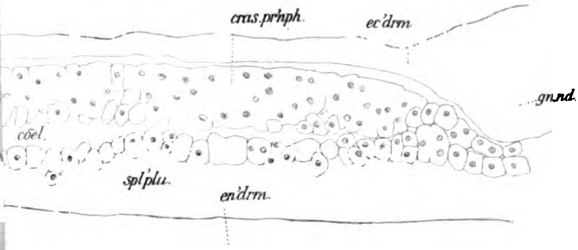

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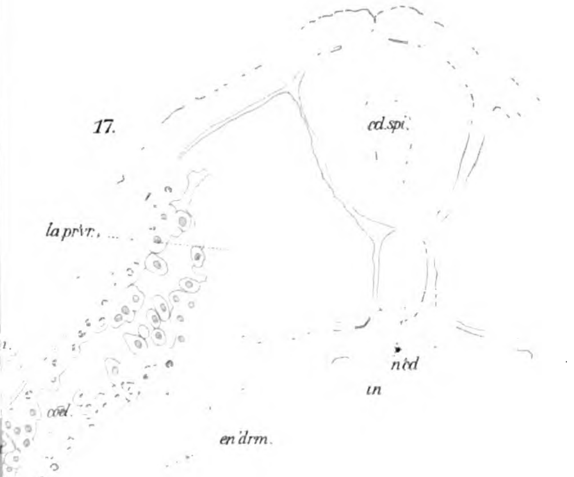

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E. Meisel, lith. Boston.

PLATE III.

Figures 18–22 and 27 are magnified 110 diameters; Figures
diameters.

Figs. 18–22. Portions of a series of cross sections through an em
In Figure 18, the pronephros of the right side i
remaining Figures, the pronephric organs of the
location of the several sections on the reconstruc
shown by the series of lines bearing corresponding

Fig. 18 shows the first nephrostome.

Fig. 19 is from a region between the first and the second nephros

Fig. 20 shows the second nephrostome.

Fig. 21 shows the third nephrostome and the anterior portion
duct.

Fig. 22 shows the segmental duct in the middle trunk region.

Figs. 23–26. Cross sections of the fundament of the segmental
terior termination, from an embryo of Stage IV.

Fig. 23 shows the duct five sections in front of its termination.

Fig. 24, three sections before its termination; *a.*, *b.*, and *c.*, cells
of the duct; *cd.*, portions of the two cells *c.* and *d.*
seen in the following section.

Fig. 25 shows the duct one section in front of its termination; *c.* a
rudiment of the duct; *b.* and *c.*, portions of two cells
lettering in Figure 24.

Fig. 26 shows the depression of the somatopleure (*f.*) directly beh
fundament of the duct.

Fig. 27. A cross section from a larva whose pronephros is sho
It shows the opening of the segmental duct into th

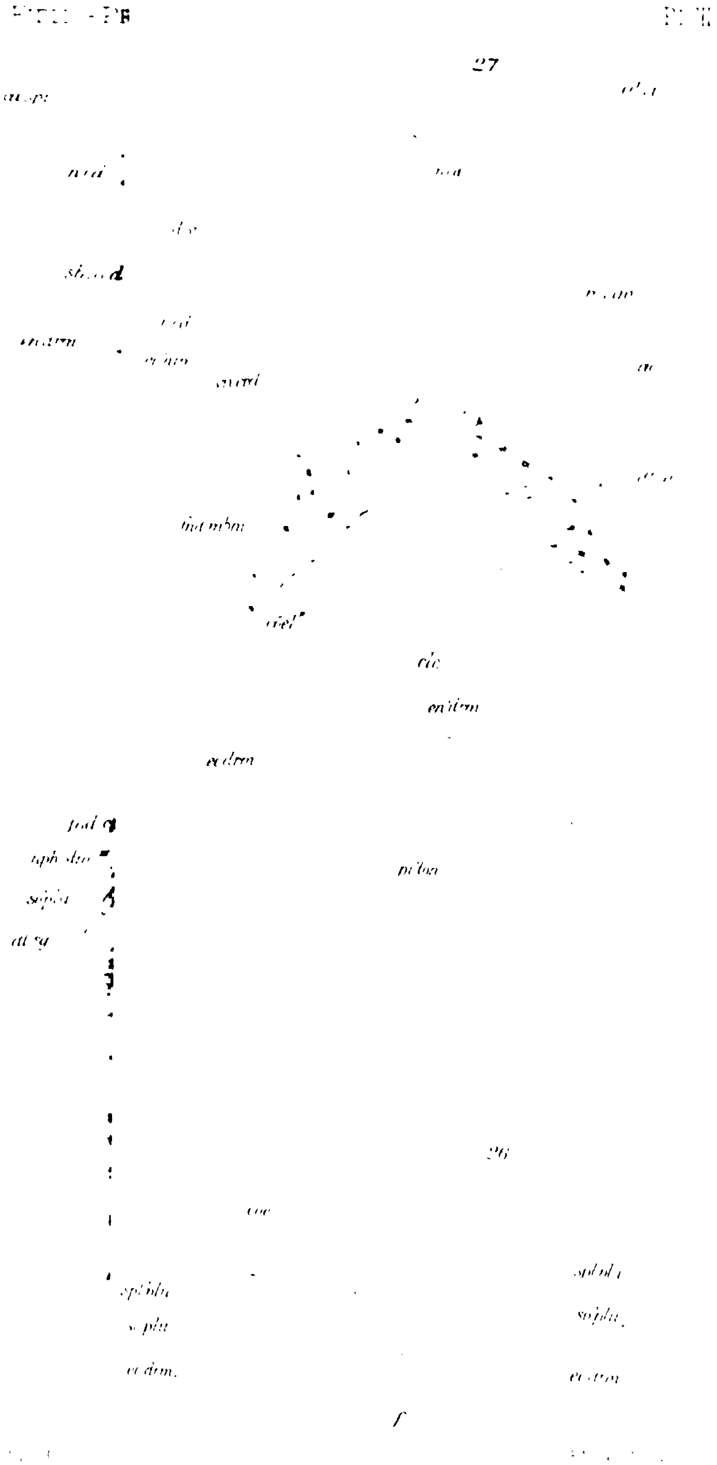
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PLATE IV.

Fig. 28. Part of a cross section through the anterior trunk region of a larva belonging to Stage VI. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 29. Part of an oblique longitudinal section through a larva of Stage IV. The plane of the section was directed so as to cut the somatopleure tangentially along the line of the three nephrostomes. Its direction is represented by the line 40 in Figure 20. × 110.

Fig. 30. Part of a cross section through the middle trunk region of a larva, from which Figure 28 was also drawn. (Stage VI.) × 110.

Fig. 31–38. A series of diagrams illustrating the convolution of the pronephric tubules. These diagrams, which are based upon reconstructions from cross sections, merely serve to show the number and approximate location of the loops in a longitudinal direction. No attempt has been made to indicate in the diagrams the changes in position undergone by the tubules in a transverse direction. The gray tint represents the common trunk and the anterior portion of the segmental duct. The first nephrostomal tubule and the collecting trunk are colored pink. The second and third tubules are represented in yellow and orange respectively.

Figs. 31–34 are from various larvæ of Stage V.

Fig. 32 is a diagram of the reconstruction shown in Figure 40.

Figs 33 and 34 represent the right and the left pronephros respectively of the same individual.

Figs. 35–37 are from various larvæ of Stage VI.

Fig. 36 is a diagram of the reconstruction shown in Figure 41.

Fig. 38 is from a larva of Rana halesina.

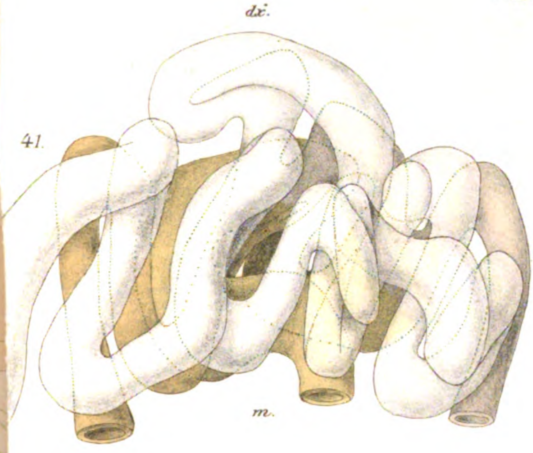
Figs. 39–41. A series of reconstructions from cross sections of larvæ in different stages of development. In Figures 40 and 41, the common trunk and the anterior portion of the segmental duct have been shaded without color; the collecting trunk and the first nephrostomal tubule have been colored pink; and the second and third nephrostomal tubules are respectively yellow and orange. × 65.

Fig. 39. Right pronephric pouch of a larva belonging to Stage IV., viewed from the median side. The ×'s represent the position of the nephrostomes. The lines 18–21 show the various levels at which the sections represented in Figures 18–21 were made.

Fig. 40. Right pronephros of a larva belonging to Stage V., viewed from the median side.

Fig. 41. Right pronephros of a larva belonging to Stage VI., viewed from the ventral side, the external face being uppermost.

41.



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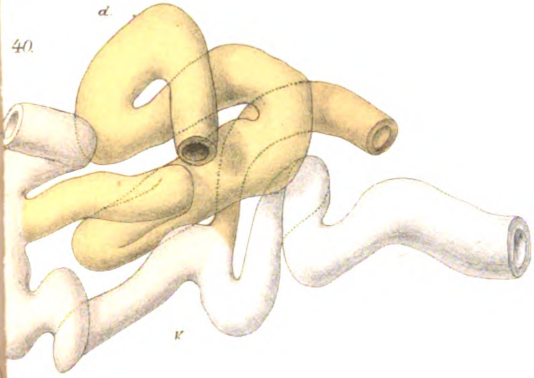

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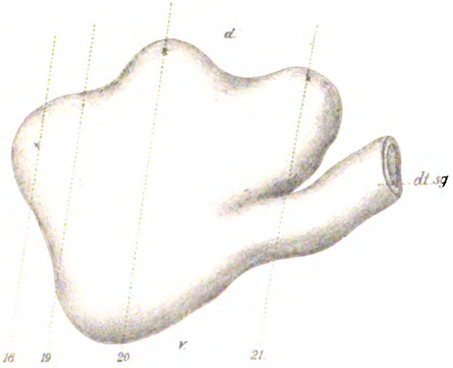

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B. Meisel lith Boston

PLATE V.

Fig. 42. A portion of a cross section through the anterior trunk region of a larva of Bufo, belonging to Stage V. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 43. A section through the rudiment of the duct near its hinder tip, from an embryo of Bufo belonging to Stage IV. × 500. Zeiss apochr. 4 mm. Oc. B.

Fig. 44. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The section shows the pronephric thickening in the region of its greatest development. × 65.

Fig. 45. A portion of a cross section through the anterior trunk region of an embryo of Rana belonging to Stage IV. The section shows the pronephric pouch in the region of the second nephrostome. × 110.

Fig. 46. An embryonic blood corpuscle occurring in the glomus of a larva of Bufo belonging to Stage V. × 955.

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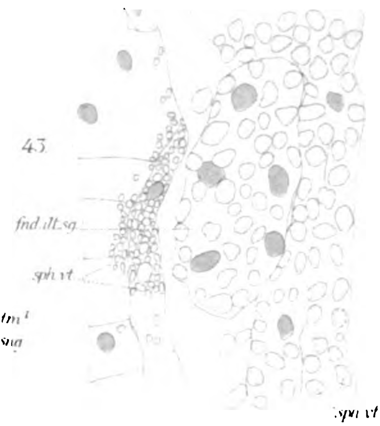
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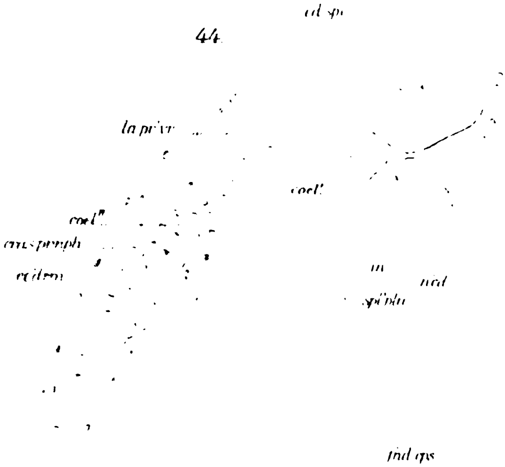
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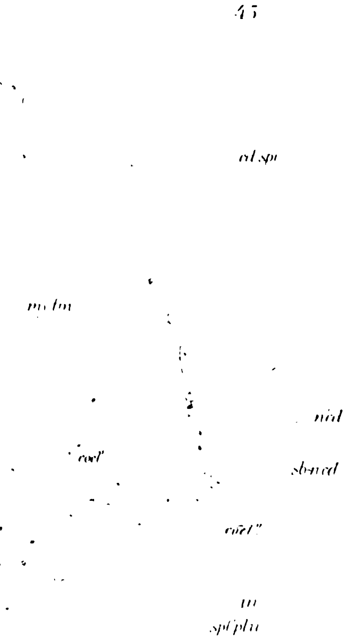
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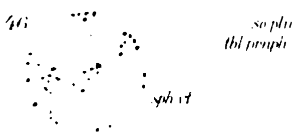
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PLATE VI.

Fig. 47. A portion of a cross section through the anterior trunk region of a larva of Bufo belonging to Stage V. The Figure shows the pronephric structures in a region between the first and second nephrostomes. × 158.

Fig. 48. A portion of a cross section through the middle trunk region of an embryo of Amblystoma belonging to Stage I. × 65.

Fig. 49. Anterior face of a cross section through the glomus of a larva of Bufo belonging to Stage V. × 470. Zeiss apocr. 4 mm. Oc. 6.

Fig. 50. Anterior face of a portion of a cross section through the right glomus of the same larva, including also the opposite peritoneal wall. × 710. Zeiss apochr. 4 mm. Oc. 12.

Fig. 51. A cross section (right side, anterior face) through the pronephros represented in Figure 37. The section passes directly in front of the third nephrostome, and shows the expanded region of the common trunk at the level of its union with the collecting trunk. × 90.

Fig. 52. A portion of a cross section through the glomus of a larva of Bufo belonging to Stage V. The Figure shows an infolding (opposite the letters *cœl.″*) of the outer peritoneal layer of the glomus. × 500.

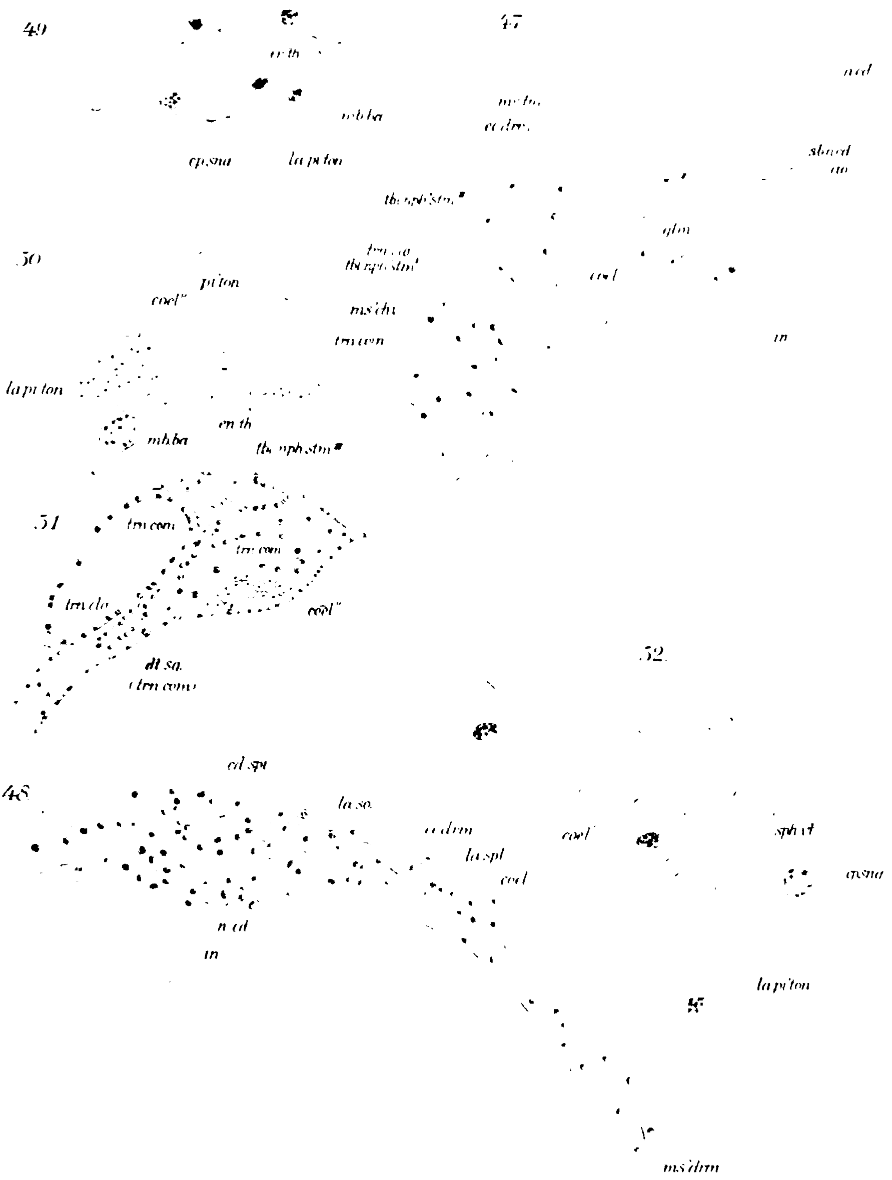
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PLATE VII.

Fig. 53. A portion of a cross section through the posterior trunk region of a larva of Amblystoma belonging to Stage VI. The section shows the fundament of the second primary mesonephric tubule (*dt. sp.*). × 90.

Fig. 54. A portion of a cross section through the middle trunk region of a larva of Amblystoma belonging to Stage VI. The section shows one of the "cords of cells" which occur between the mesonephros and the pronephros; it exhibits a case of nuclear mitosis in the peritoneum, which suggests the origin of these cells. × 500. Zeiss apochr. 4 mm. Oc. 8.

Fig. 55. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The pronephric thickening is shown in the region of the middle of Somite II. × 90.

Fig. 56. A portion of a cross section from the same series. The pronephric thickening is shown in the region of the posterior face of Somite II. × 90.

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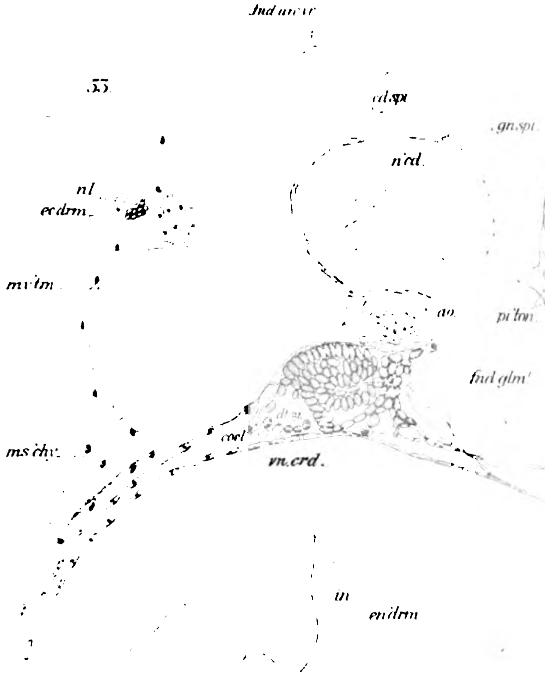
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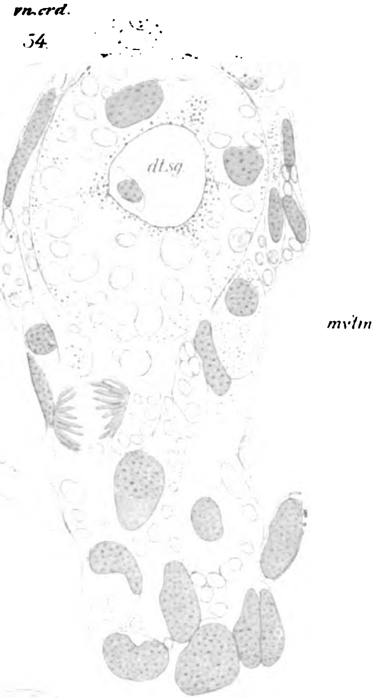
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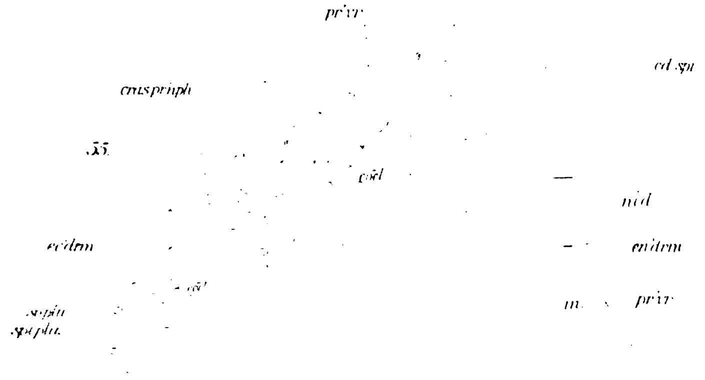
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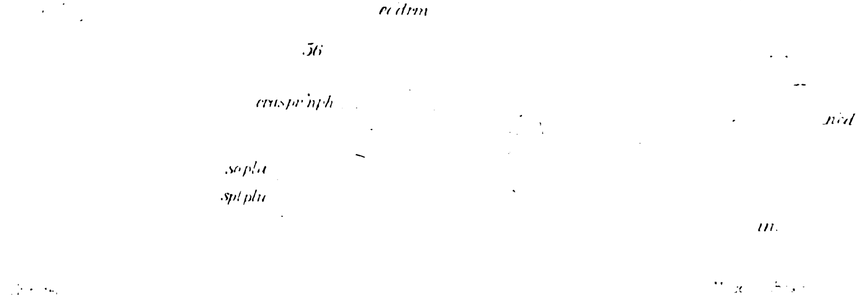
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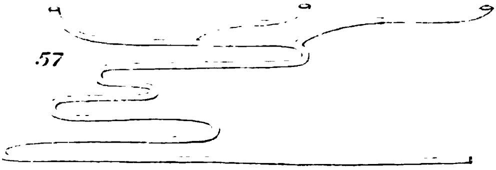
PLATE VIII.

Figs. 57–60. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage V.

Fig. 57. Reconstruction of a pronephros showing three nephrostomal tubules.

Figs. 61–65. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage VI.



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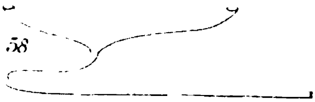

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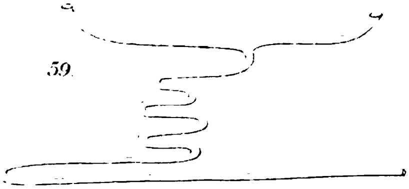

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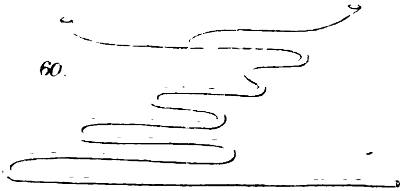

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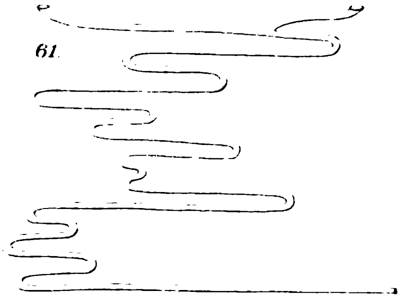

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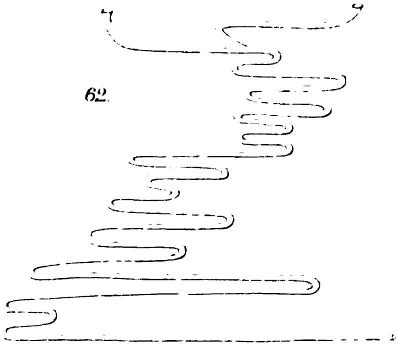

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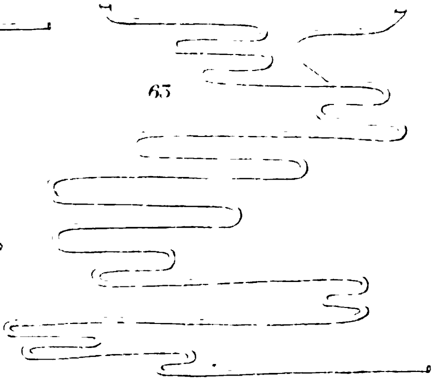

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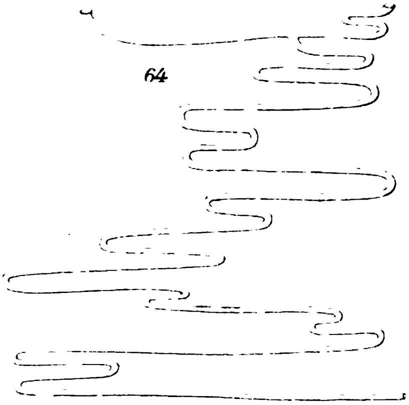

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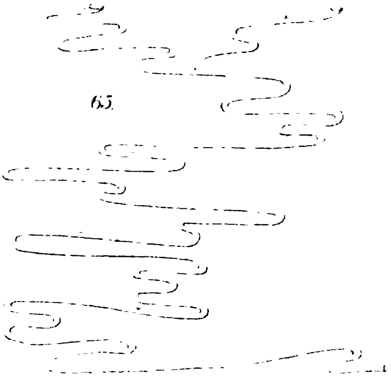

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OBSERVATIONS ON BUDDING IN PALUDICELLA AND SOME OTHER BRYOZOA.

BY C. B. DAVENPORT.

WITH TWELVE PLATES.

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No. 1.—*Observations on Budding in Paludicella and some other Bryozoa.* By C. B. Davenport.[1]

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A. SPECIAL PART.

I. Introduction.

The somewhat heterogeneous studies here brought together have been prosecuted at different times and in different places, as opportunity for getting light on the problem of non-sexual reproduction as exhibited in the group of Bryozoa has presented itself.

While studies on the fresh water species were pursued chiefly here at Cambridge, those on marine Bryozoa were made while occupying one of the tables of the Museum at the United States Fish Commission Laboratory at Wood's Holl, Mass., during the summer of 1889, and while at Mr Agassiz's Newport Laboratory during the summer of 1890. To my instructor, Dr. E. L. Mark, for many valuable suggestions during the progress of my work and the writing of this paper, to Mr. Alexander Agassiz, for the kind hospitality accorded me at his Newport Laboratory, and to Hon. Marshall McDonald, United States Commissioner of Fish and Fisheries, and Dr. H. V. Wilson, Assistant at Wood's Holl, for favors shown me while at the Wood's Holl Laboratory, I make grateful acknowledgment of my indebtedness.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVIII.

A word as to localities. The marine Bryozoa were found especially abundant at Newport on floating eel-grass in the cove and on the piles of the wharf. The embryos of Cristatella and Plumatella were found in colonies which literally covered the bottom of some parts of the south or shady side of Trinity Lake, Pound Ridge, New York. They occur especially in densely shaded and fairly deep water near the shore.

The Gymnolæmata present many difficulties to finer technique. They possess a chitinous covering, often very thick, and frequently, in addition, a calcarous skeleton. When the latter is present, picro-nitric acid mixed with sea water is a fairly good fixing reagent; when it is absent, hot corrosive sublimate was most serviceable. The objects must be transferred through the grades of alcohol with extreme caution, to prevent the collapse of the ectocyst. I used the chloroform-paraffin method of embedding in order to make transfers more gradual at this stage. Some difficulty was experienced in staining such small objects on the slide, since the tissues are very loosely associated; and on the other hand *in toto* staining is unsatisfactory in some cases, owing to impenetrability of the ectocyst. Often it was necessary to open the body cavity of each individual by means of a sharp knife or needle. The best results were obtained with alcoholic dyes like Kleinenberg's hæmatoxylin and Mayer's cochineal; although Ehrlich's hæmatoxylin was often used with success.

II. Budding in Paludicella.

1. Architecture of the Stock.

Paludicella, as is well known, occurs in quiet streams and forms stocks on the under surfaces of stones and other objects. Seen with the naked eye these stocks appear as a fine lacework, composed of constantly branching lines of individuals. Some of the stocks which I have measured are over 25 mm. in length along their greatest diameter.

When the stock is studied more carefully, it is seen that the individuals which compose it are arranged one in front of the other, forming lines. (Figs. 1, 2, 2^a.) We may distinguish (1) a single primary branch, which forms a continuous line from the oldest individual, which has been derived directly from the egg, to the terminal one; and (2) secondary branches, which arise from the individuals of the primary branch and at right angles to their axes. Typically, a secondary branch arises from both the right and left sides of each adult member of the primary branch. but in some cases the secondary branch of only one side appears to be formed. The secondary branches are composed, like the primary, of a continuous line of individuals placed end to end. These in turn give rise to tertiary branches, which run out at right angles to the right and to the left of the secondary ones, and hence parallel to the primary branches. Quaternary branches may occur in like manner, but I have never seen branches of a higher order than the fourth. All of these branches may lie in one plane, but frequently some of the lateral buds are so placed that they give origin to secondary branches which rise above the plane of the object upon which the stock lies. A study of Figure 1 and the corresponding diagram, Figure 2, reveals some additional facts. The two lateral buds of an individual do not arise at the same time, and there is a tendency for the first, and therefore oldest and most developed, secondary branches to arise alternately on opposite sides of the primary branch. This last rule has many exceptions, however.

The long axis of the individual coincides with that of its branch; the sagittal plane lies in that axis, and at right angles to the substratum. The atrial opening is near the distal end of the individual in the sagittal plane, and is turned away from the substratum. The anal aspect of the polypide is placed nearer the tip of the branch, — hence distad; the mouth, on the contrary, proximad.

A very casual observation shows that not all branches nor all individuals are of the same size. The shortest and therefore youngest branches are placed most distally, and are seen as small buds. The terminal individuals of the branches are also evidently less well developed than the more proximal ones. The adult individuals measure from 1.5 to 2.0 mm. in length and from 0.30 to 0.35 mm. in width. The younger individuals differ from the older in form also. The outline of the adult branch, looked at from the side, and disregarding the atrial opening, is formed by a series of beautiful sigmoid curves (Fig. 9). The concave and convex points of the upper and lower sides of an individual are not placed exactly opposite each other, and the lower (abatrial) side approximates more nearly to a straight line. The point at which the upper and lower curves most nearly approach each other is where the separation of two individuals takes place; that at which they are farthest apart is the middle of the zoœcium, occupied by the polypide and sexual organs. The outlines of the young zoœcia are straighter, and their breadth is considerably less than that of the adult.

From what we have already seen, the method of growth of the stock is perfectly evident: it is by the formation of new median buds at the tips of existing branches, and of new branches from lateral buds. In order to understand the origin of the individuals of the primary branches, to which subject we will first turn our attention, we must study the tips of the branches.

2. Histology of the Budding Region.

Figures 7–9 will serve to show more in detail the method of formation of new terminal individuals. We find in these cases one polypide already pretty well developed and attached to the body wall by means of the kamptoderm at about the point at which the pyramidal muscles (*mu. pyr.*) are seen to be forming. That portion of the animal which extends from about the region of formation of the muscles to a point a little proximad of the tip represents the region which will go to form the new individual. The tip itself, for reasons which will presently appear, is not to be included in the terminal individual. The tip of the branch is to be regarded as homologous with the margin of the corm in corm-building genera of Gymnolæmata. Figures 7–9 (*gn.*) also show the position of the bud which is to produce the polypide. By consulting first Figure 9, in which the polypide bud is apparent, the significance of the swellings of the body wall in Figures 8 and 7 becomes clear.

Figure 14 (Plate II.) represents a stage in the development of the polypide bud, somewhat later than that shown in Figure 9, and this may serve us as a starting point in our study of the origin of a new individual, and, first of all, of the new polypide. The whole of Figure 14, from the tip down to the neck of the older polypide (*cev. pyd.*), may be divided, for convenience, into three zones: first, that distad of the young bud, which may be called the *tip of the branch* (Fig. 14, α to β); secondly, the region of the bud itself, which may be called the *gemmiparous zone* (β to γ); and thirdly, the region between this last zone and the neck of the older polypide, which, for want of a better name, may be called the *proximal zone* (γ to δ). In the formation of a new polypide between α and β, that region will in turn become divisible into the three zones just named, exactly as the region *a* to *δ* represented the *tip* of the branch when the older polypide, whose neck is shown at *cev. pyd.*, was of the age that the younger bud is now. It will be necessary first of all to study carefully each of these three regions before treating of their origin and fate.

The *tip of the branch* consists of the two layers of cells which are found in other parts of the body wall, — the ectoderm and the mesoderm, as the cœlomic epithelium may, for brevity's sake, be called. The cells of the ectoderm at the extreme tip (Plate I. Fig. 6) are greatly elongated, forming a columnar epithelium. There are about 25 or 30 of the larger cells. They have a length of 28 μ to 32 μ, and a diameter of about 4 μ. They possess an ovoid nucleus averaging 5.7 μ by 2.6 μ, which lies in the middle of the cell but slightly nearer the cœlomic epithelium than the cuticula. It possesses a large nucleolus over 1 μ in diameter, which often appears stellate owing to the threads of plasma surrounding and proceeding from it and forming a nuclear network. As the figure shows, the plasma of the cell is filled with large, apparently deeply stained granules, some of the largest being over 0.6 μ in diameter. The coarser granules lie chiefly in the immediate vicinity of the nucleus, but are also found arranged in long lines at right angles to the surface throughout the greater part of the cell, becoming finer the farther they lie from the nucleus. A fine network can sometimes be made out between the large granules, but this appearance is more evident at the peripheral portion of the cell, where there are no large granules. At the outer and inner ends of the cells one finds large vacuoles, the largest of which are of about the same size as the nucleus; these become smaller the nearer they lie to the nucleus. In many cases the larger vacuoles are each seen to be partly filled by a body which stains slightly, and, as focusing determines, is more highly refractive than the plasma. Similar highly refracting, slightly staining granules are found in, and in fact often composing, the smaller "vacuoles." Owing to the fact that the deeply staining granules lie near the nuclei, and that the vacuolated and finely granular plasma lies more remote, there is a very marked deeply staining band occupying the middle of the ectodermal layer, and having about four tenths the thickness of the whole layer.

At the outer ends of the cells, and doubtless secreted by them, there is a cuticula about 1 μ thick. Its inner surface is sharply marked off from the underlying plasma; its outer surface is less sharp, and there are usually very minute particles of dirt attached to it (not represented in the figure). The whole cuticula forms in section a continuous band of substance, which stains deeply in Ehrlich's hæmatoxylin (but not at all in alum cochineal), and covers nearly the whole tip. Looked at from the surface after staining in hæmatoxylin, it appears uniformly dark. The mesoderm of the tip is highly modified, and a description of it will be more instructive after I shall have described the normal cœlomic epithelium, as I shall do later.

Passing from the extreme tip towards β (Fig. 14), one finds the ectodermal cells gradually changing in form, size, and structure, and becoming slightly broader, and very much shorter. Their nuclei lie near the inner ends of the cells, possess a thick "nuclear membrane," and are more nearly spherical than those of the columnar cells, but of about the same size. They each possess one very large, centrally placed nucleolus, whose diameter equals and sometimes exceeds one third that of the nucleus, and whose outline is often somewhat stellate. Outside of the nucleus in the cell body there are fewer and fewer vacuoles as we pass from the tip, but the plasma is still coarsely granular, and here, as before, these stained granules surround the nucleus. It is now the regions between cells rather than those at the inner and outer ends which remain unstained, so that the cells are separated from one another by light spaces.

The mesodermal layer becomes somewhat thinner than at the tip, that is to say, its cells are flattened. The nuclei are elongated in the axis of the branch, and average about 4 μ by 2.2 μ. They possess one spherical nucleolus, whose diameter is about two thirds of the minor axis of the nucleus. Small, clear vacuoles often with highly refractive spherical bodies are abundant in the cell protoplasm, which stains as a whole less deeply than does the ectoderm. Such highly vacuolated elements will be called *reticulated cells.*

If we study the *gemmiparous zone* at a stage considerably earlier than that shown in Figure 14, in fact at a stage in which a polypide is about to arise, we find an appearance of the layers represented by Plate I. Fig. 3. In such a region the ectoderm consists of cuboid cells about 7 μ high by 6.5 μ broad. The nuclei are large, nearly spherical, and vary in size from 3.5 μ to 6.0 μ. The largest nuclei are those in the region from which a bud is about to arise (*ex.*). One in this region (to the right of *ex.*) is 6.5 μ by 6.0 μ in diameter, with a nearly spherical, eccentrically placed nucleolus of about 3.0 μ in diameter. This nucleus is the largest which I have found in the whole tissue of Paludicella, and the same is true of the nucleolus. From the examination of many regions from which buds are about to arise, I can assert that such regions always, in Paludicella, possess large nuclei and large deeply staining nucleoli. I shall have occasion to describe similar conditions elsewhere, and to point out the probable significance of these facts. The cell body possesses a highly granular, deeply staining plasma; the inner ends of the cells, however, do not stain so deeply as the middle or peripheral portions.

The cuticula (omitted from Fig. 3, see Fig. 5) is usually somewhat different in appearance from that at the extreme tip. In section we can distinguish two layers: an outer, thicker, deeply staining layer, which is not continuous but appears broken into larger or smaller bits; and an inner, thin, non-stainable and highly refractive portion, from which the first layer is often slightly separated. This second layer is closely applied to the underlying cells, which doubtless secrete it. Looked at from the surface (Fig. 10, *a.*) the deeply stainable layer is seen to be broken into irregular polygonal pieces ranging from 2 μ to 17 μ in diameter and separated from one another by spaces ranging from 0 to 6 μ.

The mesoderm forms a loose epithelium, whose average width is less than that of the ectoderm (Fig. 3, *ms'drm.*). As a whole, moreover, it stains less deeply. In a portion of the gemmiparous zone, which lies about 180° from the budding region, the mesoderm has become so delicate a layer, if it exists at all, as not to be easily distinguishable. In the vicinity of the bud its cells have irregular outlines and extend out into the cœlom as though possessed of the power of amœboid movement. The nuclei are spherical or ovoid, smaller than those of the ectoderm, and on the whole have smaller nucleoli. The cell body is highly vacuolated. The vacuoles are not large and clear in outline, but whole regions of the cell body seem to be reduced to a non-stainable condition, and in some of these regions a fine network may still be observed.

The *proximal zone* (Fig. 14, γ to δ) is distinguished, soon after the first rudiment of the bud appears, by the diminished thickness of the ectoderm. The cells have become transformed from a columnar to a pavement epithelium. The nuclei are smaller, the nucleoli less prominent, and the cell body stains much less deeply. The cuticula is of two kinds, as before, but with this difference: the deeply staining outer part is less conspicuous, and the pieces are smaller and more widely separated. Looked at from the surface, we find an appearance like Figure 10, *c.*, in which the dark bodies represent the deeply staining cuticula. These pieces are much smaller than those of the gemmiparous zone, ranging from 0.6 μ to 9.5 μ in diameter, and separated from each other by spaces ranging from 0 to 13 μ.

3. Origin of the Polypide in the Terminal Bud.

Observation having shown that budding in Paludicella follows definite laws, we ought to be able to discover the place and time at which buds will arise; and it is necessary to do this in order to study the origin of the gemmiparous cells, and the changes which they undergo preparatory to an actual involution.

The study of tips of branches shows that the necks of the polypides of any branch all lie in one plane, and that this plane also includes the youngest polypide; also that the youngest polypides always arise distad of the next older. Knowing these facts, our observations may be confined to a short line running from the neck of the youngest apparent buds to the tips of the branches studied. The time at which to search for incipient buds and the place in the line where they will be found is illustrated by Figure 7 (Plate I.). The youngest *developed* bud is one the axes of whose tentacles are approximately parallel to the axis of the branch, and whose brain cavity, *gn.*, is not yet constricted off from that of the œsophagus. The place of origin is near the tip, immediately beyond the point at which the ectoderm changes rapidly from a columnar to a pavement epithelium.

Figure 3 is from a section across the branch in the region of an incipient bud. I have already described the conditions of the cells of this region. Those near *ex.* are larger than the surrounding ones, and show signs of cell division both in the ectoderm and mesoderm. In both cases shown in the figure, the direction of division is such as will tend to increase the superficial area of the layer in which it occurs. The ectoderm seems to be the most important layer of the two in the process of invagination which is about to take place. I think one is led to this conclusion if one considers a folding of an epithelium to be due to an increase in the area of the epithelium within a certain circumference without a correspondingly great increase in the circumference itself. Such a conception implies, first of all, mutual pressure of the cells of the invaginating epithelium. The cells of the mesodermal layer do not seem to be under mutual pressure; in some cases they are barely in contact. The cells of the ectoderm are evidently closely applied, and probably, therefore, under mutual pressure.

The one case of cell division which is occurring in the ectoderm is at the inner end of the cell. In fact, the centre of the nuclear plate is much nearer the deep end than are the centres of the adjacent nuclei. The effect of this division is to increase the area on the inner surface of the ectoderm more than that on the outer, as appears from a study of the sections shown in Figures 4 and 5. In Figure 4 certain cells lie already below the *niveau* of the surrounding ones, very much as though they had moved downward on account of this being the direction of least resistance. A later stage of this process is shown in Figure 5. Here the nuclei are already arranged in a deep saucer-shaped layer. The transition to the U-shaped arrangement of Figure 37 (Plate IV.), in which the invagination of the inner layer of the bud is completed, is not a difficult one to understand. It is to be observed, however, that the folding is of such character that it can hardly be termed a typical invagination. Comparing Figures 4, 5, and 37, it appears rather to be of a type somewhat intermediate between typical invagination and typical ingression. The cavity of the bud first arises through a rearrangement and reshaping of the cells of the inner layer of the bud. At this stage the nuclei of the invaginated region stain very deeply, and have large nucleoli.

Figure 21 (Plate III.) shows the condition of the bud at this stage as seen in longitudinal section. The proliferation which gave rise to the rudiment of the bud is shown, by a comparison of Figures 37 and 21, not to have been confined to one point, but to have occurred along a line, so that the resulting bud is boat-shaped, and not cup-shaped. The whole mass is therefore bilaterally symmetrical. Even at this early stage one can distinguish a difference in the form of the bud at the anal and oral ends. At the oral end (*Or.*) the bud passes more abruptly into the body wall than at the anal end. Later, this feature becomes more marked. This is an indication of a fact for which later stages will bring better evidence: that the formation of the bud proceeds from the oral towards the anal end, and that the increased length of the bud that one finds in the stage represented by Figure 22 is due to growth at the anal end.

4. ORIGIN AND DEVELOPMENT OF THE LATERAL BRANCHES.

The first lateral branch appears as a prominent protrusion of the lateral walls of an individual of the primary branch when the ganglion of that individual has already nearly closed, and when the bud of the next younger individual has attained a stage somewhat later than that shown in Figure 37. The zone in which the lateral buds arise lies about midway between the neck of the median polypide and the tips of its tentacles at this stage. The place of appearance in this zone is approximately 90° to the right or left of the neck of the polypide of the median individual. In one case measured, however, that shown in Figure 20 (Plate II.), the centres of the two lateral buds seemed to be unequally distant from the neck of the polypide, and each over 90° from it (approximately 100° and 110° respectively. (Compare page 3.)

A cross section of the branch through the region in which the lateral bud is arising shows that the condition of the body wall at the bud is quite different from that of the rest of its extent. Figure 19 represents a longitudinal section of a portion of the body wall passing through the non-budding region. The wall seems to consist of one layer only of cells, and a fine, non-stainable cuticula. This layer of cells is the ectoderm, for it can be traced directly into the outer layer of the tip. The mesodermal layer is not represented in the region from which the figure was drawn, but I believe it is not entirely absent from this part of the individual, for occasionally extremely flattened cells, spindle-shaped in section, may be seen lying inside of the ectodermal layer, quite sharply marked off from it by a distinct line. Further evidence of the existence of two layers is found in the fact that one occasionally sees in the flattened body wall two nuclei lying together, one nearer the cœlom than the other. The cells of the ectoderm are seen to be very much flattened (average 2.5 μ), and their nuclei are widely separated (35 μ). The nuclei are oval, and rather smaller than those near the tip. They possess a single, rather large nucleolus, which does not stain intensely. The cell protoplasm stains very little. The cuticula is about 0.5 μ thick.

If we study the body wall in the budding region, when the latter is first indicated on the surface by a marked protrusion of the outline of the zoœcium (Plate II. Fig. 15), we find that this protrusion is due to an elongation of cells. There are about twenty-two cells in this section, which are more or less thickened. Since the section figured passes through the centre of the circular thickening, and is about one sixteenth the diameter of the circle in thickness, it follows that there are over 250 cells of the ectoderm which have already at this stage become somewhat enlarged previous to evagination. The highest of these cells are the central ones, of which the largest is 22 μ high. The largest nuclei are 4 μ by 6.3 μ, which approximates the size of those in the gemmiparous region (page 6). They are placed nearer the cœlomic epithelium than the exterior, are nearly spherical, and each possesses one large nucleolus and a quite apparent network with deeply stainable nodal points. The cell body is stained as a whole rather deeply by Ehrlich's hæmatoxylin, but particularly around the nuclei. The outer parts of the central cells, however, are stained very little, and the deep ends of some of the lateral cuboid cells not at all. The network of plasma contains only fine granules, and these seem to lie in rows parallel to the long axis of the cell. The structure of the outer-layer cells, at a somewhat earlier stage, is shown in Figure 18, under a higher magnification. The network is very apparent in these large spherical nuclei, and the plasma of the cell is seen to contain coarse granules, which lie near the nuclei and stain deeply.

While the cuticula of Figure 18 is seen to be that of the normal body wall in this region, that shown in Figures 15 and 16 appears under the microscope after staining in hæmatoxylin to be of two distinct kinds: (1) that outside of the central region, which is highly refractive and not at all stained; and (2) that which lies immediately over the central elongated cells of the bud, which is also highly refractive but stains deeply. In fact, the central cuticula resembles in every way that already described for the tip of the branch, and shown in Plate I. Fig. 6. Moreover, it has other points of resemblance to the latter. It does not stain at all in alum cochineal; the outer boundary of the branch is often uneven at this place (Fig. 16); and particles of dirt are often found adhering to it, while the rest of the cuticula is comparatively free. The difference in staining properties of the central and lateral cuticulas indicates that the former undergoes with age a change in its chemical properties; the irregular outer boundary and the adhesion of dirt particles seem to indicate that the newly formed cuticula is viscid. The mesoderm of the stage of Figure 15 consists of a single loose layer of subspherical cells of the two kinds already noticed, reticulated and non-reticulated. The series of Figures 18, 15, and 16 shows the behavior of columnar cells in the formation of a typical outfolding as distinguished from the slipping in of cells to form the polypide (Figs. 3, 4, and 5).

In stages later than that of Figure 16, the tip of the branch becomes further removed from the body wall of the median branch. The cells at the tip always retain their elongated columnar condition. A polypide is soon formed on the upper part of the body wall immediately behind the tip, exactly as in the case of the median branch. A septum is very early formed, cutting off the lateral from the median individual, and the lateral secondary branch becomes the median primary one of new individuals (Plate VI. Fig. 58).

We have already traced out the origin of the polypide of the median branch from the mass of cuboidal cells near the tip; it remains to determine whether the cells which give rise to the lateral branch can be traced directly back to the cuboidal cells of the tip, or whether they have arisen from the flattened epithelium of the general body wall and secondarily acquired their plump "embryonic" character.

Figure 18 (Plate II.), to the cellular conditions of which I have already referred, shows an early stage of the lateral branch, and Figure 20, *gm. l.*, shows on a smaller scale the different cellular conditions in the body wall in the region of two lateral buds which are yet far from showing external signs of evagination. The cells are cuboid and much higher than those of the adjacent body wall. Have they been so ever since they were derived from the tip, or have they secondarily become so ? I believe that these cells have never been flattened pavement epithelial cells, for the following reason. All ectodermal cells of the body wall near the tip are cuboidal; if these cells have only secondarily acquired this form, they must have passed through a stage in which they were flattened epithelium. Now, if these cells could be distinguished by greater thickness from the cells of the surrounding body wall, at a time at which the latter cells had only just begun to emerge from the cuboidal condition to become differentiated into the pavement epithelium of the body wall, it would follow that, even though they had secondarily increased in size as a result of an impulse preparatory to evagination, and even though they would have been at a stage only a very little earlier indistinguishable from the other cells of the body wall, yet they would never have passed in this case through a flattened condition, because at a stage only a very little earlier the whole body wall was composed of cuboid cells.

The conditions which I have set as the criterion of our problem are fairly realized in Figure 17, which represents a portion of the body wall of a median branch which extends from the gemmiparous region above to the thickened body wall of the nascent lateral bud below (*gm. l.*). It will be seen, by a comparison of the body wall of this region with that shown in Figure 19, which is taken from the same individual farther from the tip, that even the most differentiated part of the body wall of Figure 17 is in a relatively indifferent condition as compared with the pavement epithelium of the ectoderm of Figure 19, in which the mesoderm, indeed, has become so thin and insignificant as scarcely to be visible. We may, therefore, maintain that the ectodermic cells of the body wall have only just begun to lose their cuboidal condition to become pavement epithelium, and therefore conclude, in accordance with the argument just presented, that the cells of the lateral bud (*gm. l.*) have never passed through a stage in which they were flattened epithelium. It is evident, also, that the *Anlage* of the second lateral bud is also derived from near the tip, because, as in Figure 20, we find two lateral regions of cuboidal cells.

5. Development of the Body Wall.

It is, of course, almost impossible to gain direct evidence upon the place of origin and method of development of the body wall, and one is therefore forced to the collection and weighing of circumstantial evidence. Braem ('90, pp. 127, 128, 131) believes that the body wall (the cystid, in Nitsche's sense) has a double origin in Paludicella: "Ein Theil des Cystids zwar vor dem Polypid, ein anderer aber erst später angelegt und zwar aus der polypoiden Knospe selbst entwickelt wird." The part developed from the bud of the polypide is the elliptical region of the body wall, whose main axis lies in the sagittal plane and which has the neck of the polypide at the distal focus and the attached ends of the retractor muscles and the parietovaginal (or pyramidal) muscles lying in the proximal circumference, — the greatest part of the ellipse thus lying oral of the atrial opening. The evidence for this conclusion Braem finds in the following facts, which my own observations confirm: "The great retractor first appears in the angle between the oral part of the polypide bud and the cystid wall [cf. Figs. 23, 24, *cl. mu. ret.*]; then its cells gradually become elongated, and as its point of origin retreats farther and farther from the polypide, it finally appears as a bundle which joins a point lying between the mouth of the polypide [neck of the polypide] and the inferior septum with the pharynx, and, as I believe, also with the cardial part of the stomach" (p. 125). Compare the muscles at the left end of Plate I. Fig. 8. Further on he says: "Die Parietovaginalmuskeln [pyramidal muscles] erscheinen an der Knospe zuerst in Form zweier seitlichen Leisten, in welchen die einzelnen jugendlichen Fasern senkrecht zur Längsaxe verlaufen. Indem sich alsdann lateral von der Knospe das Cystid durch Neubildungen erweitert, werden die Fasern verlängert und die beiden Bündel treten in Flügelform deutlicher zur Rechten und Linken der Mündung hervor. Ihr Ursprung an der Cystidwand rückt nun von der Mündung immer weiter ab und gelangt schliesslich auf die gegenüberliegende Seite, wo er anal und lateral seinen definitiven Platz findet." Compare Plate I. Figs. 7–9, *mu. pyr.*, and Plate VI. Fig. 63, *mu. pyr.* From these observations Braem ('90, pp. 127, 128) concludes: "So scheint es sicher, dass auch hier ein grosser Theil des definitiven Cystids, das ja zum anderen Theil schon vor der polypiden Knospenanlage entwickelt war, aus dem Material dieser letzteren hervorgeht. Das folgt namentlich aus der Art und Weise, wie sich die Muskeln bilden. . . . Auch hier würde, wie bei den Phylactolæmen, oral vor der Knospe nach dem Retractor hin, ein grösseres Gebiet der Leibeswand der Knospenanlage entstammen, als seitwärts und hinten."

An analysis of the facts has led me to conclusions differing somewhat from those of Braem; namely, that all or nearly all of the cells of the body wall (cystid) are derived from the tip of the branch or from the immediate descendants of cells so derived. The number of cells contributed to the formation of the body wall by the neck of the polypide is much smaller than Braem has suggested, and probably insignificant in amount. The retreat of the points of origin of the retractor and parietovaginal (pyramidal) muscles may be in part accounted for by the normal growth in area of the body wall, and in part by the actual movement of the point of origin with reference to the cells of the body wall. These conclusions rest upon the following circumstantial evidence.

Owing to the small number of cells in the body wall at the tip, and the comparatively slow growth of the cystid, karyokinetic figures are much less frequent than in the polypide. Quite a long search has therefore not afforded cases enough to enable me to draw any perfectly satisfactory conclusions as to just where, and where only, growth was taking place. I have, however, seen nuclear division occurring in the elongated cells of the extreme tip, rather more abundantly in the cuboidal cells between the extreme tip and the gemmiparous zone, and most abundantly in the gemmiparous zone, but here evidently having to do with the origin of the polypide, muscle cells, etc. Proximal to the gemmiparous zone, I have noted few cases of nuclear division excepting about the neck of the polypide. It seems probable that the cells of the tip of the branch are not to be regarded as forming a differentiated organ whose elements rarely divide, but as quite capable of adding new cells to the body wall. On the other hand, there is by no means a *Scheitel* in the botanical sense, but the cells added to the body wall continue for a time to divide vigorously, and finally give rise to the polypide, to the *Anlage* of the lateral branches, and to the body wall. The cells belonging to the proper cystid then cease to divide rapidly.

I have already shown how the cells of the tip secrete a cuticula, which becomes gradually replaced by a second cuticula secreted beneath it as the body wall attains its adult dimensions. It appears as though the first cuticula were secreted by the cells of the tip *only*. This being so, since the area of the body wall increases, this first cuticula must either stretch to cover the enlarged area, or else it will fail to cover it and appear as isolated patches upon the body wall, and these isolated patches will become more and more widely separated as the area of the body wall increases. This latter condition seems to be the one realized in this case. The presence of the old cuticula is easy to demonstrate, since it stains deeply in hæmatoxylin; and it may be easily distinguished from that formed later, for with the same reagent this stains not at all. Figures 6, 11, 12, and 13 show different appearances of the cuticula at different parts of the body wall. At the extreme tip (Fig. 6) there is a continuous deeply stained band of cuticula. In Figure 11 it no longer appears quite homogeneous, but is darker at some places than at others. The ectoderm is here composed of cuboidal cells. At a later stage of development the ectodermal cells have become very much flattened. A thin, unstainable, more deeply lying cuticula has already begun to form, and the outer deeply stainable cuticula is seen to be broken up into bits. Figure 13 is from the adult body wall. The ectoderm is flattened. The inner cuticula has attained a great thickness, and the outer cuticula is represented by only a few deeply staining patches. One attains a similar result by studying the surface of a stained individual. Figure 10 shows the condition of the outer cuticula at intervals along the same branch from the gemmiparous region *a* to a nearly adult region, *d*. The bits of cuticula become more and more widely separated and smaller, as I have already described in detail on page 7. Here, then, we have not merely an interesting case of replacement of one cuticula by another to meet the needs of the enlarged body wall by a method which has no parallel, so far as I know, in any other group of animals, but for the specific purposes of our problem *a criterion of growth of the body wall* quite as satisfactory as karyokinesis, and much easier of application.

Let us apply this criterion in our attempt to answer the question, Is that portion of the body wall lying between the neck of the polypide and the points of origin of the pyramidal muscles (Plate VI. Fig. 63, *b–a*, *b–c*) derived wholly from the neck, or is it merely the result of interstitial growth of that part of the original cystid which was preformed in the neck region? If the first condition is true, we should expect to find no indications of the outer cuticula secreted by the tip of the branch; if the second, we should expect to find the outer cuticula broken into bits, and underlaid by the inner lately formed cuticula. Figure 63 shows clearly the deeply stained outer cuticula here separated into bits, and, to my mind, thereby proves that this part of the cystid has had an origin similar to that of the rest of the body wall. Moreover, a comparison of the portion of the section figured with the remainder (and this comparison has been made on many sections from several individuals) shows that the parts of the cuticula about the neck are indeed rather smaller and farther removed from each other than at the opposite side of the branch; but the difference in this respect is not very marked, and may well only signify that there is a more rapid growth of the body wall in the vicinity of the neck of the polypide than at the opposite side.

But how then do the points of origin of the pyramidal muscles come gradually to move away from the neck of the polypide at which they arose, in order finally to lie so that the muscle fibres are nearly parallel? If the points of origin remain fixed with reference to the surrounding cells, they can hardly come to lie *absolutely* closer together, but only *relatively* so by growth of the body wall between these points and the neck. If, however, we find that in older individuals the points of origin are not only relatively but absolutely closer together, we are driven to the conclusion that these points move relatively to the surrounding cells. To decide whether the points of origin come to lie closer together behind the neck *absolutely* or only *relatively*, I measured cross sections of four individuals through the region of the neck in which the muscle fibres showed evident differences of length, and therefore of age. I may preface a table of these measurements with the statement that the muscles first appear plainly differentiated at a stage when the polypide is well formed (Fig. 7, *mu. pyr.*), and that the growth of the body wall in circumference is not very considerable after this time. The numbers indicate measurements in micra: —

	No. 1.	No. 2.	No. 3.	No. 4.
Distance on periphery between origins of muscles, atrial side	150	154	187	260
Distance on periphery between origins of muscles, abatrial side	297	286	264	220
Total length of periphery	447	440	451	480

The distance on the "atrial side" signifies the distance measured over *a*, *b*, *c*, Figure 63 (Plate VI.). The length of the remainder of the section is the distance on the "abatrial side."

From these measurements it appears that the "origins" of the pyramidal muscles approach each other absolutely, — a condition which Braem's hypothesis cannot explain, and which can be reasonably interpreted, it seems to me, only by assuming, however unique and difficult of conception such a condition may be, that the points of origin move relatively to the surrounding cells of the body wall. (Compare also the movement of parietal muscles referred to on page 29.[1])

It is not necessary to assume that the increase in extent of the body wall after the polypide is first formed is due to the addition of cells from the neck. The change in form of the ectodermic cells from a columnar to a pavement epithelium must alone cause a great increase in the extent of that layer. Some measurements that I have made seem to me to prove that the area of the body wall does increase greatly, even outside the region whose growth Braem attributed to the addition of cells from the neck of the polypide. Thus, in one case, the distance from the distal end of the polypide bud, which becomes the neck of the adult, to the point of origin of the young retractor muscle was 0.17 mm.; from the same point to the septum separating the young individual from the next older was 0.27 mm. In the next older individual, from the neck to the origin of the retractor muscle was 0.72 mm.; from the neck to the septum was 2.0 mm. Thus assuming that the older individual passed through a stage exactly equivalent to that in which we find the younger, the distance from the neck to the origin of the retractors has increased 0.55 mm., and from the origin of the retractors to the septum 1.18 mm. The first distance is that in which Braem has assumed the body wall to grow by additions from the neck of the polypide, and this assumption was apparently made to account for the increase in extent of this region; but the area between the origin of the retractors and the septum, which is outside the region to which additions such as Braem contemplates could have been made, has grown in this case very considerably more in extent. This case is not a typical one, however, for we rarely find the distance from the origin of the retractor to the septum to be so great. In general, from observation of a number of cases, I should say that in the adult the distance between the neck of the polypide and the origin of the retractors, is to the distance between the latter and the septum about as 5 : 4, and that therefore the growth of the first region is slightly greater than that of the second. From the fact, however, that the cells around the neck of the polypide for a long time retain a somewhat embryonic character, and may quite frequently be seen in division, this was to have been expected. The conclusion which I draw from this last series of conditions is, then, that it is unnecessary to suppose the addition of cells from the neck of the polypide to account for the fact that the origin of the retractors is carried backward from the polypide. Normal growth of the body wall, such as occurs elsewhere, is quite sufficient to account for it.

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[1] Professor Mark has called my attention to a discussion of the movement of the fixation-point of a muscle in Mollusks by Tullberg ('82, pp. 26, 27, 44). This author says that he has undertaken no special investigation of the method of migration, but concludes that this motion must result from the absorption of the inner muscle fibres as new ones are formed on the outside. I do not find any evidence of such a process in Paludicella.

To recapitulate. That portion of the cystid lying in the vicinity of the neck can hardly be derived from the neck alone, for the cells still show adhering to them the cuticula which they derived from the tip of the branch. It is not necessary, in order to account for the movement of the origins of the muscles away from the neck, to suppose that the circumcervical region is derived in that way; for (1) the origins of the pyramidal muscles actively migrate away from the neck to a certain extent, and (2) the normal growth of the body wall is sufficient to account for the carrying backward of the origin of the retractors.

From the facts already gained it seems clear that the ectocyst (cuticula) is first formed at the tip, and then, to meet the wants of the growing colony, this is replaced later by a cuticula of different chemical composition, which becomes thicker as the body wall grows older. At a late stage we find a separation of the thick cuticula itself into two layers, of which the outer one is much the more highly refractive.[1] (Plate II. Fig. 13; Plate III. Figs. 26, 29.)

6. DEVELOPMENT OF THE POLYPIDE.

We have already (pages 8, 9, Figs. 5, 14, 37) seen how the foundations of the polypide are laid by the ingression of cells of the outer layer of the body wall pushing before them the mesoderm, and how, finally, those cells arrange themselves in a boat-shaped mass to form the inner layer of the bud (Plate III. Fig. 21), which possesses no actual cavity, and is constantly separated from the external world by the ectoderm which remains behind to form the neck of the polypide. Even when a cavity is formed later, it does not communicate with the exterior until the permanent atrial opening has arisen. The earliest differentiation in the bud is, as mentioned by Allmann ('56, p. 36), the formation of a cavity which is to become that of the atrium. This cavity is first formed at an early stage as an extremely slight fissure in the midst of the inner layer. Figure 22 shows a longitudinal section of this stage. Cell division is taking place throughout the whole mass, but especially at the neck of the polypide, *cev. pyd.* The position of the cavity is represented by the central non-nucleated space, and this gives rise, as the later history of development shows, to the atrium and the pharynx.

Figure 23 represents a stage which is doubtless of short duration, for I have found it only twice. The bud is much more developed at the anal end than in the last stage, and there is a second cavity below the atrium, from which it is separated by a line of nuclei. This is plainly an early stage in the formation of the *alimentary tract*, which thus first appears at the anal side of the bud, as in Phylactolæmata, and is progressively formed towards the oral end. An appearance similar to the one figured would be given by a slightly oblique section of a later stage; but this section is strictly sagittal, and no trace of the lumen appears in adjacent sections. I have found a similar condition in a series of longitudinal sections at right angles to the sagittal plane of the bud (Plate IV. Figs. 39 and 40). Figure 39 shows that the atrio-pharyngeal cavity is first developed at the anal end, and in Figure 40, which is three sections (about 15 μ) below Figure 39, the anal end only of the alimentary tract is formed. It is worthy of notice that the cells of the mesodermic layer of the bud are often greatly vacuolated at this stage, as in Figures 39 and 40, *vac.* Braem ('90, p. 126) says of this stage: "Die der Resorption dienenden Darmabschnitte, Magen und Enddarm, werden gemeinsam angelegt, indem auf jeder Seite der Knospe eine Längsfalte die Wandungen nach innen und gegen einander zu einbiegt, worauf die benachbarten Theile des inneren Blattes verschmelzen und so durch eine Art Abschnürung das primäre Knospenlumen in den vorderen Atrialraum und die hintere Darmhöhle getrennt wird." While I thoroughly agree with this statement, the additional fact of the formation of the tract *progressing from the anal towards the oral end* is interesting, in that it shows that the process of formation of the organ in Paludicella is fundamentally similar to, although differing slightly in detail from, that of the Phylactolæmata. Figure 24 shows in sagittal section a still later stage in the development of the alimentary tract. A cross section of this stage is seen in Figure 30 (Plate IV.), in which the separation of atrial and gastric cavities is demonstrated. The inner layer of the bud is here seen to be separated from the ectoderm by a distinct line, and, to a certain extent, even by the mesoderm. The distal (oral) part of the cavity of the alimentary tract next becomes considerably enlarged to form the stomach (Fig. 25). The outer layer of the bud, *ms'drm.*, penetrates between the stomach and the atrium, and a depression is formed at the bottom of the atrial chamber which will give rise to the œsophagus. Even at this stage the œsophagus is not in communication with the stomach, but their cavities are separated by two layers of cells of the inner layer of the bud. These two layers become those of the cardiac valve (Plate IV. Fig. 36, *vlv. cr.*). By a further comparison of Figures 25 and 36 it will be noticed that, whereas in the earlier stage, as in Endoprocta, there is no cœcum to the alimentary tract, in the later stage the cœcum has already begun to form, as in Phylactolæmata, by an outpocketing of nearly the whole of the lower wall of the stomach. (Compare also Plate I. Figs. 7, 8, and 9.)

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[1] Such a two-layered condition of the cuticula was long ago described by Reichert ('70, pp. 265, 266) for Zoöbotryon. He distinguished "eine *äussere, festere,* stärker lichtbrechende und sprödere Schicht und die *innere weichere.*" Realizing that the "ectocyst" or cuticula undergoes many changes in form, — formation of lateral buds, of septæ or communication plates, and increase in size of the stolon, — he suggested, without having observed the process, that probably during these changes the more rigid outer layer disappeared and was replaced by the inner softer one.

Very soon after the establishment of the alimentary tract, and between the stages shown in Figures 24 and 25 in sagittal section, there begin to appear organs which have a very considerable phylogenetic significance; namely, the lophophoric ridges, ring canal, and tentacles.

The *lophophoric ridge* is a fold which surrounds the mouth, and from which at intervals tentacles arise. The ridge, however, arises before the tentacles. The general position of the ridge, as well as its method of origin, may be learned from an inspection of a series of sections of the age of those shown in Figures 31–34. In a section lying near the oral end of the bud (Fig. 33), one finds two spaces, — a lower, which is that of the stomach, and an upper, the œsophagus and atrium. This upper space is broader above than below, and the cell layer which lines it is thick below, but above, or nearer to the body wall of the budding individual, it is thinner. The transition from one condition to the other is quite abrupt, and is marked by a salient curve (*loph.*). In a section near the anal end of the bud (Fig. 31), it will be seen that here too the inner layer is thick below and thin above. The characters mentioned are still more strikingly shown in the median section, Figure 32. That the differences in thickness of different parts of the inner layer are recently acquired modifications of an earlier simpler condition is indicated by comparing Figure 32 with Figure 30, which is from a younger bud. The series of points (*loph.*) of transition from thick to thin epithelium forms on the reconstructed polypide a curved line, convex above. This line is the ridge of the young lophophore (compare Fig. 25, *loph.*). I have said that the lophophoric ridge arises before the tentacles. The evidence for this assertion is found in a series like that referred to above, where, although the ridge exists along the entire side of the atrium, one finds nascent tentacles in the middle region only (Figure 32, left hand).

As Figure 25, of a later stage than Figures 31–33, shows, the lophophore curves downwards rapidly at the anal end, so that it here lies at right angles to the axis of the rectum, but does not extend at all beyond the anus. Orally, there is in the median plane only the slightest trace of the lophophoric ridge. By the formation of this ridge in the wall on each side of the atrial chamber, the original atrio-pharyngeal cavity has become separated into two regions. The space lying within or below the ridge forms the pharynx and the intertentacular space; that lying without and above, the atrium of the adult. (Plate III. Fig. 25; Plate IV. Fig. 32, *atr.*) Since the lophophore curves rapidly downward to the anus and does not extend behind it, the act of cutting off the lower part of the atrio-pharyngeal cavity from the upper (atrium proper) does not continue behind the anus, which therefore opens directly into a part of the atrium. This part has the form of a compressed funnel, and is bounded behind and laterally by the kamptoderm, and orally by the hinder ends of the lophophoric ridges, and also, since the latter do not meet in the median plane, by the pharyngeal cavity. Thus it has come about that the anus, which at first opened into the common atrio-pharyngeal cavity of the bud, has now, in the separation of the two regions, come to lie near their point of division posteriorly, but to open distinctly into the atrial cavity. The more pronounced separation of the part of the atrial cavity into which the anus directly opens from the remainder of the atrium takes place much later, and will be described further on.

In Figure 33, the *ring canal* (*can. crc.*) is seen to be already formed. At this stage it is found on one side only, the left, if one looks at the polypide from the tip of the branch. It occurs in only four sections (each 5 μ thick), being found on the next section behind Figure 33, and on two sections nearer the oral end. At its oral extremity, it terminates blindly as a thickening of the outer layer of the bud; at its anal end, one sees cells of the outer layer extending out partly over the canal, but failing to enclose it; in the next section the mesoderm is undisturbed. In similar sections of an older polypide (corresponding in age approximately to Plate IV. Fig. 35), the canal is found on both sides, and near to the oral end, but at about the middle of the series (cf. Fig. 35) it is found to open again into the body cavity. I therefore conclude that the ring canal makes its first appearance at the base of the lophophore in a region just oral of the middle of the polypide. Exactly how it arises, whether by a growing together of the lips of a shallow furrow formed from the mesodermal layer, or by the formation of a pocket, which, elongating, penetrates between the inner and outer layers of the polypide at the base of the nascent lophophore, I have not been able to determine. Two facts induce me to believe that the later formation of the canal oralwards results from the penetration of a sac-like mass of mesodermal cells between the two layers of the polypide at the base of the nascent lophophore. One usually finds, (1) as in Figure 33, *can. crc.*, a double mesodermal wall between the lumen of the canal and the cœlom, and one layer between the former and the inner layer of the bud; and (2) at the oral blind end of the ring canal a number of loose cells (occasionally dividing) representing the blind end of the pocket and lying between the inner and outer layers, both of which are intact.

Braem ('90, p. 50) describes the formation of the ring canal in Phylactolæmata as taking place in the manner just suggested for Paludicella. His studies were made, he says, preferably on statoblast animals. Nitsche ('75, p. 358) concluded that in Phylactolæmata the ring canal was first a furrow, whose lips fused, and my own study ('90, p. 129) has led me to the same conclusion. Since reading Braem's account I have looked over some of my own sections of Cristatella again. Certainly the process is not so clear in the buds of the adult colony as in the statoblast embryo which Braem figures. Nevertheless the series of sections ('90, Plate IV. Figs. 33–38) given as evidence of my statement still seem to me capable only of the conclusion I drew from them. Perhaps the processes may be different in detail in the two cases; certainly the two explanations are not fundamentally dissimilar.

The ring canal being established in the oral part of the polypide, it grows forward, as I have said, and, secondarily, the canals of both sides meet in the median oral line and their lumina become confluent (Plate VI. Fig. 52, *can. crc.*). From what has already been said, it is clear that the lateral parts of the ring canal are not now continuous with each other behind. They become so only after the formation of the tentacles.

The *tentacles* arise upon the lophophoric ridge at a stage a little later than that represented in Plate IV. Figure 32. At the stage represented by Figure 35, however, the tentacles have begun to form, as indicated by the fact that in the series from which this figure was taken the fold into the upper part of the atrium appears now deep, now shallow, according as the section passes through the length of a young tentacle, or only through the lophophoric ridge between the tentacles. The position of the section (Fig. 35) is about the middle of the series, corresponding to Figure 32.

By a comparison of Figure 35 with Figure 32 in respect to the tentacles, it will be apparent, first of all, that the lophophoric ridge itself has been heightened and that this heightening has been effected, not by a deepening of the fold existing in Figure 32, the lips of the fold remaining quiescent, but by a movement downwards of the outer lip (*) of the groove which is to form the ring canal. The movement is of course accompanied by an increase in the length of the kamptoderm, *kmp. drm.* This growth of the lophophoric ridge naturally does not result in making the tentacles project farther above the ridge. Their elongation must take place quite independently of the former's. The lophophoric ridges have now become elongated folds lying upon the right and left of the polypide, which at this stage has a very compressed appearance (Plate IV. Fig. 41). The folds occupy the position of the ridges, and therefore do not lie throughout their whole extent in one plane, but oralwards are nearly parallel to the body wall (Plate III. Fig. 25), analwards trend nearly at right angles to it. It results from this fact, that one cannot see the anal tentacles when looking at the polypide from the side of the body wall to which it is attached. Figure 41 (Plate IV.) shows also that no tentacles have yet made their appearance at the oral ends of the two lophophoric ridges.[1] The tentacles are here seen to be arising in two long rows, and so that those of one row are placed opposite the intertentacular spaces of the other. There are six tentacles in each row. The rows are not continuous with each other oralwards or analwards.

The separation of the atrial and oral cavities, begun by the first formation of the lophophore, is, now that the tentacles have arisen, much more pronounced. Other changes now occur in this region, which produce an extensive modification in the form of the polypide.

One of the first of these changes is the close approximation and finally fusion of the anal extremities of the lophophoric ridges oralward of the anus. A stage in this is shown in Figures 43 and 44 (Plate V.), which are sections in the position of the lines *43*, *44*, of Figure 25 (Plate III.), but through a slightly older polypide than that represented by Figure 25. The section shown in Figure 43 passes across the rectum, grazes the outer lip of the ring groove of the anal tentacles, and finally cuts, nearly longitudinally, one of the middle tentacles of the row. The two lophophores are not yet completely fused in front of the rectum. In Figure 44 (compare Plate III. Fig. 25, *44*) this break in the continuity of the lophophore is more prominent.

By the completion of the union of the lophophores in front of the anus, the rectum is quite cut off from communication with the intertacular space. It now opens only into the thin-walled, funnel-shaped depression of the atrial cavity.

Pari passu with this operation the stomach and rectum are being more completely separated from the pharyngeal cavity by the penetration of a double layer of mesoderm between these regions from each side, and a fusion of the corresponding layers of the two sides. Finally, the walls of the stomach and pharynx become separated from each other by a part of the cœlomic cavity, as in Plate IV. Figure 36. This process of separation of the alimentary tract proceeds analwards, and finally the rectum is far removed from the œsophagus.

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[1] Compare Plate IX. Figure 77, which is a superficial view of the young lophophore from Flustrella, in which the process is similar to that in Paludicella, only the down curving of the anal tentacles occurs later than in the latter case.

The anus thus comes to lie farther outside of the anal tentacles. Finally, the ring canal, which is formed progressively farther and farther analwards, follows the fusion of the anal ends of the lophophores, and thus completes the canal behind the œsophagus. (Plate IV. Fig. 36; Plate VI. Fig. 53, *can. crc.*)

The anal part of the ring canal is doubtless not merely a groove, but a tube; but the ring canal is not closed at this, and probably not at any stage throughout its entire extent, for in Plate VI. Figure 52, two sections below Figure 53, an opening is shown to exist on each side (at *can. crc.*), putting the cavities of the ring canals and the cœlom into communication with each other. These openings lie at the sides of and slightly above the ganglion (*gn.*, Fig. 52); a position exactly comparable with that of the openings in the ring canal of Phylactolæmata, which leads from the cœlom into the lophophoric arms on the one hand, and into the circumoral part of the ring canal on the other.

By a comparison of Figure 41 (Plate IV.) with the sections shown in Figures 60–62, it will be seen that the row of tentacles has undergone a change of form: from being laterally compressed, it has become circular. This change of form has not resulted from an increase in the number of the tentacles, for at the stage of Figure 41 there are six tentacles on each side already formed (the sixth not visible), and there are in front of the mouth spaces already reserved for the two additional tentacles. There are also, probably, two nascent tentacles at the anus, although these are little developed, making a total of 16. In Figure 61 there are only 15 tentacles; moreover, the actual diameter of the tentacular corona in the sagittal plane is less than at the earlier stage of Figure 41. This change of form is perfectly normal, all young polypides having tentacles arranged in two parallel rows, and adult polypides having a circular lophophore.

These changes in the form of the tentacular corona are correlated with important changes in the direction of the axes of other organs. These changes may be understood by comparison of Figures 25 and 36, together with the assistance of Figures 7–9, all of which are oriented in the same manner. In Figure 25 the points fixed by the cardiac valve (*vlv. cr.*) and anus (*an.*) lie in a line which is approximately parallel to the body wall. In Figure 36 the line passing through the same points makes an evident, but not very large, angle with the body wall. This line has undergone, then, a slight change of position only. The axis of the anal tentacles lies in both cases nearly parallel to the body wall, and so does the neural wall of the pharynx. The oral tentacles, on the contrary, whose axes in the earlier stage are directed perpendicularly to the body wall, lie in the later stage with their axes parallel to the wall; and the base of the lophophore, which in the earlier stage trended at its oral end parallel, at its anal perpendicular to the body wall, in the later lies throughout its whole extent in one plane perpendicular to the body wall. The axes of the oral tentacles have rotated through an angle of nearly 90° relatively to most of the other organs of the polypide. The cause of this rotation must evidently be sought in unequal growth in different parts of the polypide. A comparison of the length of the kamptoderm on the anal side in Figures 25 and 7 indicates that it has grown more in length than on the oral side. This excessive growth would tend to rotate the line *vlv. cr.* — *an.* to a position perpendicular to the body wall. Since this rotation has not occurred to so great an extent as was to have been expected, we must look for a compensating growth on the oral side of the polypide, between *vlv. cr.* and the neck of the polypide, which shall be nearly equal to the excessive growth of the anal kamptoderm, and which must be *outside* of the oral kamptodem. These conditions of location are fulfilled only by the oral wall of the œsophagus, and it is by change of position and growth of this wall that the extension of the anal kamptoderm is nearly compensated for on the oral side of the polypide. By this growth in the wall of the œsophagus the oral part of the ring canal has been brought to lie over the anal part, the sagittal diameter of the tentacular corona has been reduced, and the compressed lophophore has been transformed into a circular one.

Concerning the number of tentacles, Dumortier et van Beneden ('50, p. 46) observe that in the adult there are ordinarily 16, although individuals with 18 tentacles occur not infrequently, an observation which Kraepelin ('87, pp. 98, 99) confirms. In addition to these numbers, I have found 15 and 17. The growth of the odd tentacle is quite interesting. The sections reproduced in Figures 60–62 (Plate VI.) will serve to illustrate a condition which I have quite frequently found in a polypide with 17 tentacles. In this particular series there are only 15 tentacles. The successive sections abundantly demonstrate that the odd tentacle (*) is anal in position, and that it is younger than any of the others; thus in Figure 61 its tip is cut, in Figure 60 there are only 14 tentacles visible, and these are found in the two following sections. Since there are six sections which pass through the tentacles, and the odd tentacle is found in only three of these, it follows that it is only about one half as long as the others.

The *nervous system* arises, as in Phylactolæmata, by a depression in the floor of the common atrio-pharyngeal cavity, in the region which later becomes the anal surface of the pharynx. As in Phylactolæmata, we first see a shallow pit (Fig. 25, *gn.*). This appears to become deeper, sinking downward and somewhat toward the cardiac valve (Fig. 78, *gn.*). Finally it becomes constricted off from the wall of the œsophagus, and then appears as a cellular mass closely attached to it and surrounded exteriorly only by mesoderm. (Plate I. Fig. 8; Plate VI. Figs. 52, 53, *gn.*) Even before the closure of the ganglionic pocket is completed, the formation of the circumœsophageal nerve, first described by Kraepelin ('87, pp. 62, 63) in the adult, begins.

Figure 52 (Plate VI.) shows a transverse section of a young polypide in which the ganglion is solid, and not provided with a large cavity as in Phylactolæmata. There is a small cavity in the upper part of the ganglion, and this is not yet wholly closed from the œsophagus. The ganglion is continuous with a pair of hornlike processes (*n.*) which partly enclose the œsophagus, and at a later stage do so wholly (Plate IV. Fig. 36, *n'.*) The cells of these horns are found dividing in unusual abundance. The horns lie next to the digestive epithelium, and between it and the mesodermal lining of the ring canal. From the method of growth, and from the sharp line of separation between the tips of the horns and the surrounding tissue, there can be little doubt that the circumœsophageal nerve of Paludicella, like the lophophoric nerves of Phylactolæmata, arises as an outgrowth of the brain.

Serial sections show that the ganglion suddenly diminishes in size immediately below the point at which the circumoral nerves arise, but one can trace a layer of cells continuous with the brain downwards for ten or fifteen micra farther, to near the cardiac valve. At this point one can still see nuclei of a third layer lying between the digestive epithelium of the valve and the mesoderm. It seems to me, therefore, that this may be regarded as a gastric nerve, which seems to originate by a single root and later to give rise to two nerves, one of which lies on either side of the cardiac valve.

7. Origin of the Muscles.

a. Retractor. — After its first formation the bud becomes elongated in the direction of the axis of the branch. The derivation of this elongated stage from the much shorter earlier one might be effected in one of two ways: either, first, by the ingression of cells from the ectoderm at points successively more and more remote from the point of primary invagination, the additions to the length of the bud being made by a continuation backwards of that process by which the first foundations were laid; or secondly, by cell proliferation at the point of first invagination pushing the oral end of the buds farther and farther from the neck of the polypide.

I think there can be little doubt that the second is the method by which the bud becomes elongated; and for the following reasons. (1) The oral end of the bud, on the supposition of continued invagination of the body wall, should become very gradually of less diameter, and transverse sections at that end should exhibit the ingression (potential invagination) of cells which were observed in the earliest stage; but as a matter of fact the oral end is abrupt (Plate III. Fig. 22, 23, *Or.*), and no stages of ingression are to be found there. (2) On the first assumption, the inner layer of the bud should be at all points in equally close relation to the ectoderm of the body wall; on the second, the inner layer should be closely connected with the ectoderm at the neck of the polypide (Plate III. Fig. 22, *cev. pyd.*), but elsewhere it should be sharply separated from it. As a matter of fact, a sharp line can be distinguished, in a sagittal section, separating the inner layer of the bud from the overlying ectoderm at all points except at the neck (anal part) of the polypide (Plate III. Figs. 22–25). Moreover, cross sections of the anal part of the bud show the inner layer passing directly into the ectoderm, and oralward the outer layer of the bud tends to penetrate more and more between the ectoderm and the inner layer. Therefore I conclude that the inner layer of the bud is constantly augmented by cell proliferation in its mass, and especially at the neck of the polypide, and this explanation also accounts for the active cell proliferation observed at the neck in Plate III. Figure 22, *cev. pyd.*

Since the polypide later becomes attached to the body wall by the comparatively narrow "neck" only (Figs. 7, 9, *cev. pyd.*), a separation of the oral part from the body wall has to take place. This process begins at the oral end. In its earliest stages it is indicated by the sharp separation of the inner bud-layer from the overlying ectoderm, and the partial penetration of the mesoderm on each side into the space between these two layers (Plate IV. Fig. 30, *ms'drm.*). At a later stage the mesoderm may be seen as a single cell layer lying between the ectoderm and the inner layer of the bud midway between the oral and anal ends (Plate IV. Fig. 32, *ms'drm.*), and as a double cell layer at the oral end of the bud (Fig. 34, *ms'drm.*). It is from these cells at the oral end of the bud that the retractor muscles are to arise (Plate III. Figs. 23–25, *cl. mu. ret.*). As the oral end of the kamptoderm and œsophagus to which their inner ends are attached moves away from the ectoderm, and as the area of the latter itself increases, the two ends of the cells move farther and farther apart, and the young muscle cells become drawn out into spindle-shaped muscle fibres. (Plate III. Fig. 25, *cl. mu. ret.*; Plate IV. Fig. 36, *mu. ret.*) The retractor thus arises unpaired and remains so at its origin, but nearer its insertion in the ring canal and œsophagus one can distinguish a division into right and left masses. The adult muscle fibres consist of two parts at least, the inner contractile portion and an outer less modified protoplasmic portion, which can be traced over the whole of the first part, but is most evident around the nucleus, where it has a granular appearance.

b. Pyramidalis. — At about the stage of Figure 25 (Plate III.) one finds, on cross sections of the branch which pass through the neck of the polypide, that the mesoderm of the body wall on each side of the neck is greatly thickened, and that its closely packed cells, which lie three or four deep, have become somewhat elongated. Cell division is quite common in the ectoderm of this region, and by it the area of the circumcervical region is increased and the two ends of the muscle fibres are carried farther apart, one end remaining attached to the neck of the polypide and the other moving towards the abatrial surface. I have given reasons above (page 16) for believing that the abatrial ends of the muscles are not carried towards the abatrial side passively, and solely by the growth of the body wall, but that the ends move relatively to the cells of the body wall. A somewhat late stage in the development of the pyramidalis is shown in Figure 63 (Plate VI.). Nearly the whole of the mesoderm of the body wall has here been transformed into muscle cells. The insertion of the muscles is in the mesoderm of the neck of the polypide. (Plate VI. Fig. 63; Plate V. Fig. 45.)

c. Parietal muscles first make their appearance at about the stage of the terminal individual of Plate II. Figure 14, immediately below the bud and to the right and left, i. e. so that the muscles, which usually arise paired, have their long axes parallel to the sagittal plane and perpendicular to the long axis of the branch. They arise from cells of the mesoderm, most of which in this region are filled with vacuoles, and often project into the cœlom. But in my opinion the muscle cells do not themselves arise from such vacuolated cells, for at even an earlier stage (corresponding to Figure 21, Plate III.) one can distinguish thickened patches of elongated cells in the mesoderm which are undoubtedly the young muscle cells; but they do not show the slightest traces of being vacuolated, and in fact are sharply distinguished from the adjacent cells by their uniformly granular appearance and their deeper coloration.

Braem ('90, pp. 124, 125) has already stated that the parietal muscles arise in pairs, and come to traverse the cœlom, not remaining in the body wall. The truth of this statement I can confirm in the case of the parietal muscles first formed, which lie near the future septum. Plate V. Fig. 42 shows the origin of the muscle fibres on both sides of the branch. They have already migrated into the cœlom. As Braem plainly states, the component parts of this pair of muscles, developed from the mesoderm, migrate towards each other and finally fuse into one unpaired mass, as we see in Plate III. Figure 26. It is perfectly evident, in this case at least, that both ends of two muscles originating far apart migrate in some manner towards each other so that the corresponding ends come to lie close together. Such a migration cannot be accounted for merely by growth of the body wall. The ends of the muscle fibres must move relatively to the body wall.

When the muscles have reached their permanent positions in a diameter of the branch, we find their ends attached to the cuticula. As the muscle fibres stain deeply in hæmatoxylin, they can be distinctly traced through the vacuolated and poorly stained cells of the body wall (Plate III. Fig. 26). Figure 29 shows a bit of the wall mechanically separated from the cuticula, the end of the muscle fibre remaining in place. Fine lines can be distinguished in the contractile, deeply staining portion of the fibre. The surface by which attachment is effected appears very slightly crenulated on longitudinal sections of the muscle fibre. I could not distinguish any structural peculiarity on the part of the cuticula to which the muscle was attached, — nothing to indicate how attachment is effected.

Freese ('88, pp. 15, 22, Fig. 11) has described a similar method of attachment of the muscles to the cuticula for Membranipora.[1]

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[1] My friend, Dr. G. H. Parker, tells me that a similar method of attachment of muscle fibres to the cuticula occurs in *Crustacea*. According to Tullberg ('82, pp. 27, 44, 45), the adductor muscle fibres are in Mollusks attached to the cells of the ectoderm. The same condition as in Mollusks seems to exist in Annelids (Eisig, '87, pp. 25, 36).

At a later stage smaller bundles of muscles arise successively toward the neck. These muscles are free from the body wall at their middle region. They do not usually pass through the cœlom in a diameter of the branch, however, but rarely subtend as chords an arc of more than 120°. As Braem supposed, such muscles, although arising later than the most proximal pair, originate in a similar manner to them (Plate VI. Fig. 55). The mesoderm is very thin at the region at which they are first seen, and they are quickly discerned by their larger nuclei and prominent cell body. At a later stage they have grown much longer, and become freed from the body wall at their middle part.

As is well known, there are two *funiculi* in Paludicella, called by Allman respectively anterior (nearer the atrial opening) and posterior. The origin of the funiculi of Paludicella was observed by Dumortier et van Beneden as long ago as 1850. They say (p. 54), "La couche muqueuse une fois formée s'étend rapidement dans l'intérieur et touche bientôt par son extrémité inférieure les parois opposées de la loge. Les cellules muqueuses dont le tout est encore composé contractent de l'adhérence dans cet endroit, et c'est ce qui donne naissance au muscle rétracteur de l'estomac [= funiculi]." Allman ('56, p. 36, Plate XI. Figs. 7–9) also describes and figures very clearly and correctly this process, and Braem ('90, p. 127) has recently confirmed their observations.

It is perhaps unnecessary to redescribe the more evident part of this process, the contact of the polypide with the abatrial wall of the branch. The mesoderm of the bud comes into contact with that of the body wall, the cells of each of the two layers become attached to the other, and by the withdrawal of the polypide the attachment persists at two points forming a long drawn out string of tissue. Figures 36^a and 38 (Plate IV.) are contributions to a knowledge of the finer details of this process. Apparently the upper funiculus is developed earlier than the lower, as I have always found it longer at about this stage. The lower funiculus at present consists of only the two mesodermal layers of body wall and polypide intimately united. The funiculus itself consists of a cord several cells thick; but I believe these certainly to be derived from the mesoderm only. Very early some of these cells show an appearance of highly refractive and deeply staining fibres, which I interpret as muscular differentiation (Plate IV. Fig. 38, *fun. su.*), so that the funiculi must be regarded as partly muscular in function. As in Phylactolæmata, these fibres lie near the axis of the funiculus. Braem ('90, pp. 66, 67,) has demonstrated that the muscular fibres of the funiculus of Plumatella pass directly into the muscularis of the body wall. It is interesting to find them persisting in the funiculus of Paludicella, beneath the mesodermal covering, although there is apparently no muscularis developed in the body wall of this region.

8. The Formation of the Neck and Atrial Opening.

This is the last act in the history of the polypide that I shall consider. The body wall around the neck of the polypide continues to possess a less differentiated character than the remaining portion for some time after the oral tentacles have undergone their revolution. One still sees the cells of this region dividing, and the body wall is gradually protruded at this point above the general level. (Plate II. Fig. 14, *cev. pyd.*) The neck of the polypide to which the kamptoderm is attached consists, at a somewhat earlier stage than that just referred to, of a disk of greatly elongated columnar cells in the centre of which there is a distinct notch caused by the presence of shorter cells at that point. (Plate VI. Fig. 63 *b.*) At the inner ends of the columnar cells of the neck lies a flat epithelium quite sharply marked off from the latter, but which is nevertheless undoubtedly derived from the same source as the columnar cells and the inner layer of the bud. This flat layer is directly continuous with the inner layer of the kamptoderm. At a later stage, the columnar cells of the ectoderm become elongated still more, and lose their staining capabilities at their outer ends. Still later one sees them arranged in the form of a cup whose cavity is separated from the outside world only by a cuticula which becomes slightly invaginated at this point. The cells are soon found with their long axes perpendicular to the edge of the cavity they line.

There is one point that I have not been able to determine; namely, how the new cuticula, which is certainly formed at the ends of the cells which lie next to the cavity, becomes continuous with the old cuticula of the non-invaginated body wall, as it is in Figure 50 (Plate V.). The presence on the new unstainable cuticula of the remains of the stainable one, whose origin I have already discussed at length, may serve as a guide to the limits of the old cuticula. The new cuticula is being secreted by cells lying deep in the inner end of the neck, and apparently in one rod-like mass. Unfortunately, I lack stages between this figure and Figure 45 (Plate V.), which shows the neck of a nearly or quite adult polypide cut lengthwise. The solid cuticular rod has now become a hollow cylinder, whose inner (deep) edge is embedded in the deep-lying cells of the neck. Moreover, one finds superficial to the cuticula of the general body wall a second cuticular cylinder, which is free at its outer end, but at its inner end fuses with the surrounding cylinder of cuticula. This inner cylinder, which is probably formed, as Kraepelin ('87, p. 40) suggested, by splitting of the delicate cuticula at the base of the marginal thickening (Randwulst), has been compared by Kraepelin to the "collare setosum" of Ctenostomes. The *Randwulst* itself I believe to be the equivalent of the Diaphragma of Nitsche, as I shall try to show later.

At the deep end of the neck (Fig. 45), the inner layer of the bud is seen to be continuous with the ectoderm. The region of transition may be called the atrial opening, *of. atr.* Surrounding the atrial opening is a fold in the ectoderm, and between the layers of this fold is a thin, non-stainable homogeneous layer, slightly more refractive than the surrounding protoplasm. This membrane extends also a short way into the kamptoderm, and here lies between its two cell layers. Embedded in this homogeneous membrane in the fold, one can distinguish still more highly refractive bodies, *spht.* On account of their form and high refractivity, I believe these to be muscle fibres cut across. The homogeneous membrane has also the same general appearance and relation to the muscularis as the so-called supporting membrane of Nitsche, and it is the only representative of that structure that I have found in Paludicella.

9. Development of the Communication Plate.

In their description of Paludicella, Dumortier et van Beneden ('50, p. 40) say: "Il se compose de plusieurs loges ou cellules placées bout à bout . . . en sorte qu'il n'y a aucune communication entre les différents animaux." Also Allman ('56, pp. 114, 115) refers to the presence of a perfectly formed septum separating the cavities of adjacent "cells." To Kraepelin ('87, p. 38) belongs the credit of having first carefully studied this structure in the adult by means of sections. He came to the conclusion from the appearances which he figures (cf. my Plate V. Fig. 49), that there are small canals passing through the nearly homogeneous central mass, and therefore "dass wir in dem ganzen Apparat eine Vorrichtung zu erblicken haben, durch welche Nährstofflösungen des einen Tieres mittels siebartig wirkender Cautelen in die Körperhöhle des Nachbarindividuums übergeführt werden."

The descriptions of Kraepelin concerning the structure of the "Rosettenplate" are confirmed by my own observations, and seem to justify his conclusions concerning its function. The development of the organ has not, however, been carefully observed heretofore. Korotneff ('74, Plate XII. Figs. 1 and 2) gives figures to show this process, but I have never seen any such circular groove surrounding the branch as he figures. In all cases the two layers of the body wall form a circular fold, in which, however, there is never, even at the earliest stages, a space between the ectodermal layers, nor any infolding of the cuticula as Korotneff ('75, p. 369), according to Hoyer's rather incomplete abstract, maintains (Plate V. Fig. 47). When the circular fold has advanced until only a small pore remains, by which the cavities of the older and younger individuals are kept in communication, the mesodermal cells at the angle of the fold begin to undergo a metamorphosis both in form and histological character. In the first place they become much elongated and extremely attenuated, passing from one surface of the septum to the other, and forming the lips of the pore. In the second place their plasma becomes first deeply stainable, and later, in addition, homogeneous and highly refractive. These metamorphosed cells form what may be called the *teeth* of the plate. They are derived wholly from mesoderm.

The cells in the upper mesodermal layer next increase rapidly in number and size, and the number of teeth is also augmented (Plate V. Fig. 48). The metamorphosis of the cells extends still farther away from the communication pore, and involves the lower mesodermal layer; but, apparently, each cell of the latter is metamorphosed only to a slight depth within its cell wall (Fig. 51), whereas in each of the upper cells the ends which project into the communication pore are modified through and through (Fig. 46). At a later stage (Fig. 49) the metamorphosed part of the cell seems quite sharply cut off from the active part, and the slits between the metamorphosed teeth are considerably reduced. Nevertheless, I believe a transfer of fluids may still occur between them, for even in the adult communication plate one can trace continuous lumina when the cells are by accident torn off from the "teeth" which they have produced. It is important to note that the nuclei are not destroyed in the cell metamorphosis. Some lie above, others below the pore, and become deeply stainable. The ectodermal layers of the communication plate secrete a cuticula between them. This is thinner than that of the body wall, and does not extend, of course, to the centre of the communication plate, but ends in a thickened ring, whose diameter is about one tenth the diameter of the plate, or, absolutely, about 9.4 μ.[1]

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[1] Reichert ('70, p. 267) first carefully described the Rosettenplate of Ctenostomes in Zoöbotryon, and the organ in Paludicella must be regarded as homologous with it. The central circular hole in the cuticula of Zoöbotryon is from 7 to 10 μ in diameter, and from one ninth to one seventh that of the entire plate. Similar

10. RÔLE OF THE MESODERMAL VACUOLATED CELLS.

Allman ('56, p. 36) observed that at the time a lateral branch was well formed, and before the origin of the polypide, the internal outline of the body wall was uneven, and he figures (Plate XI. Fig. 4) very large cells lying on the inside of the body wall. Korotneff ('74, Taf. XII. Figs. 1–3, '75, pp. 369, 370) progressed a step farther, and recognized a distinction between large, coarsely granular cells projecting into the cavity of the bud, especially near the tip, and the surrounding epithelial cells. Braem ('90, p. 126), finally, has described them more accurately. He finds cells filled with numerous granules in the youngest branches of the colony. Immediately around the bud, such cells are less abundant; probably, he says, because their granules have been absorbed in the process of formation of the polypide. He compares the granules with the yolk spherules of the statoblast cells, and believes that they are to be regarded as food matter.

My observations and conclusions, achieved independently of Braem's, fully confirm his. I have succeeded, moreover, in obtaining some additional evidence as to the function of these cells, a subject to which I have paid some attention.

First as to the *distribution* of the cells, and their frequency in different regions. We can best get an approximate idea of this by counting the number of the reticulated cells in each section of a series which involves a young polypide and the regions immediately above and below it. It is not possible to do this with perfect accuracy, because there is no sharp line of distinction between reticulated and non-reticulated cells; but I have made the count without prejudice, and I believe as fairly as possible. When the bud of the polypide has reached about the stage shown in Plate III. Figure 28, the number of reticulated cells seems to have nearly reached a maximum. In the series from which this figure was taken there was an average of 4.8 reticulated cells to the section in the ten sections distal of the bud. There was an average of 11.2 reticulated cells to the section for the twenty sections which passed through the bud, and 11.2 for the eleven sections proximal of the bud in the region

perforated organs have been described by Smitt ('67, p. 426), Nitsche ('71, pp. 420–422), and Vigelius ('84, p. 26) for Flustra, by Freese ('88, p. 7, 13, 14) for Membranipora, by Ostroumoff ('86^a, p. 18) for Lepralia, by Claperède ('70, p. 160) for Bugula and Scrupocellaria, by Ehlers ('76, p. 14) for Hypophorella, and by Joliet ('77, p. 222) for Bowerbankia. Nitsche alone ('71, p. 455) has had anything to say upon their origin, and this apparently not the result of direct observation.

at which muscle fibres were arising. A similar series through a slightly older bud gives for the same regions respectively 5, 14, and 13 cells per section. In series through older buds, a rapid decline in the number of these cells occurs so that at the stage of Figure 30 (Plate IV.) there is an average of only about 3.1 cells per section through the bud, and about 2.2 immediately below. These reticulated cells are not very numerous in the region of the bud at the time this is about to arise, as a look at the sections Figures 3 and 4 shows. One finds reticulated cells in the mesoderm at the tip, and most abundantly at a rather early stage in the development of the bud. The number of these cells diminishes as one leaves the young individual to pass into the next older of the same branch. In the adult such cells are rather rare; so rare, in fact, that Kraepelin ('87), who studied with care the body wall of the adult individual, makes no mention of them. Nevertheless they do occur in the cells which are to go into the lateral branch (Plate II. Fig. 15), as well as elsewhere on the body wall. The place in which one finds the reticulated cells most abundant, however, is in the young *lateral* branches near the time when the polypide bud is about to arise. Here every cell of the mesoderm is greatly enlarged, and filled with the vacuoles (Plate VI. Fig. 58). These are very apparent upon a surface view of the branches. Reticulated cells occur not only in the mesodermic cells of the body wall, but also in those of the polypide bud, which were, indeed, only lately a part of the mural mesoderm (Plate III. Fig. 28, Plate VI. Fig. 56). Thus, in general terms, we may say that the reticulated cells of the mesoderm are chiefly confined to regions in which there are young buds developing; and since these arise at intervals only, there is a periodicity in their appearance, — a time of maximum development followed by one of decline, then one of reproduction of such cells in the ends of branches culminating in another maximum, and so on.

Turning our attention now more particularly to the *structure* of these reticulated cells at the period of their best development, we find (Plate VI. Figs. 56, 57, 59) that they possess a large nucleus lying at the deep end of the cell and containing a relatively large nucleolus, and that this is surrounded by a granular protoplasm with included vacuoles. It is very common to find the nuclei in various stages of division, and thus it is frequently seen as a mass of chromatic substance without any nuclear membrane or nucleochylema. The vacuoles, which in the more regular cells lie in a semicircle nearly peripheral (the nucleus being at the centre), are highly variable in number, some of the cells containing as many as 20 to 30. They often appear as perfectly clear homogeneous spaces, but more frequently at this stage contain a spherical body, which frequently fills the entire vacuole and is more refractive than the surrounding plasma (Fig. 59). Not unfrequently one sees a less refractive, clear space, surrounding the highly refractive body (Fig. 57).

The description just given corresponds to the condition seen in a terminal branch whose polypide has attained the development of that shown in Figure 28 (Plate III.). At the time immediately preceding the origin of the bud, the cuboidal cells of the mesoderm show traces of vacuolation, but their form and size have suffered no appreciable disturbance. This vacuolation of cells proceeds hand in hand with the development of the bud, and one first notices the homogeneous, highly refractive bodies in the vacuoles when the bud is well established. At about the time the alimentary tract has become formed, the reticulated cells begin to show signs of degeneration. The highly refractive bodies have disappeared, and the skeleton of the cell which remains becomes very irregular. As already stated, the number of reticulated cells also decreases, until, at about the time of "rotation" of the polypide, there are few reticulated cells in the mesoderm, but these few are filled with vacuoles and their highly refractive bodies.

The conditions of the mesodermal cells at the tip are slightly different from those found elsewhere. Usually, instead of many small vacuoles, one finds only one or two which fill almost the entire cell, — sometimes perfectly homogeneous in structure, sometimes containing small highly refractive granules.

These appearances I believe to be explicable only upon the assumption that *the mesodermal cells are capable, at the time at which the young polypide is arising, of imbibing the fluids of the body cavity and storing them up for the purpose of supplying the rapidly growing cells of the bud with nutrition.* It is desirable to show reasons for believing, first, that the contents of these cells are nutritive matter; secondly, that this has been taken up from the body cavity; and, thirdly, that it is supplied to the bud for its nutrition.

It must be admitted that the strongest argument for the belief that these are absorbing cells is derived from a comparison of the appearances which we find in these cells with those described for Protozoa, and by Metschnikoff ('83, Taf. I. Figs. 18–35) for mesodermal trophic cells. At the same time, it must be acknowledged that similar cells are found in other cases where the function is believed to be not ingestive, but excretory, as in the chlorogogen cells of Annelids, as shown by Kükenthal ('85), Eisig ('87, pp. 751–762), and others, and indeed even in the cells of cœlomic epithelium. Eisig ('87, p. 752) has already clearly expressed how, in view of the many cases of high excretory activity of peritoneal and blood cells demonstrated by him, "künftighin bei der Beurtheilung gewisser Zelleneinschlüsse erst genau festzustellen sein wird, ob man est mit *von aussen aufgenommenen* (gefressenen), oder aber mit von der Zelle *ausgeschiedenen* Producten zu thun habe."

A criterion for judging this matter may be found, in the first place, I believe, in this: that the products of excretion increase with the activities of the cells, and are thrown out, usually in the shape of concrements, either *from* the cell or *with* the cell into the cœlom; whereas bodies taken in from without for digestion decrease with the activities of the region. In the second place, vacuoles are less characteristic of excretory tissue than of imbibitory. But vacuoles are the important feature of the reticulated cells in Paludicella, and the highly refractive bodies are less constant phenomena. As for the latter, they are not found in the later stages, nor in the earliest. Moreover, these bodies differ from excretion concrements in this, that they are always transparent, often almost indiscernible in the vacuole, except by their higher refractiveness, and there is no sharp demarcation between cases of vacuoles filled by such bodies and those the contents of which are less highly refractive. The degree of refractiveness is variable, at one end of the series grading off into the undifferentiated fluid of the vacuole. What significance is to be assigned to these highly refractive bodies in the vacuoles? There are two reasons why I do not believe that they represent solid food particles devoured as such by the mesodermal cells. First, I do not find such highly refractive bodies lying loose in the body cavity before the stage at which they first appear in the cells; and, secondly, one can find all gradations between less highly refractive vacuoles and highly refractive ones (which I have assumed to be entirely filled by one highly refractive body), and between the latter and vacuoles containing a small body surrounded by a broad, clear area. I believe, therefore, that the vacuoles are rather cavities filled with chemically different nutritive fluids, which are acted upon differently by the reagent.

I have assumed that the contents of the vacuoles represent material taken up from the body cavity, because it seemed most reasonable to look there for the source of their supply. The ectoderm is covered on its outer surface by an apparently continuous cuticula, so that food cannot be gained from the outside world directly. It is, moreover, not unreasonable to suppose that some of the products of digestion elaborated by the adult polypides of the colony pass through the wall of the alimentary tract in solution, and thus into the body cavity, from which they may be taken up by the mesodermal cells at the growing part of the body wall. Nor is there anything unreasonable in insisting that the body cavity functions, in these animals without blood-vessels, as a hæmo-lymph system, for in many animals with incomplete vessels, such as Arthropods, Hirudinea, etc., it evidently does so to a certain degree. Moreover the constant motion of the fluids of the body cavity of Bryozoa points to the same thing. It is conceivable that the food in the digestive cells might be distributed throughout the body wall without passing into the body cavity, since all parts of the body wall are continuous with the digestive epithelia of the polypides of the colony. Two considerations make it improbable that the cells of the tip gain their nutrition in this manner from the digestive cells of the youngest functional polypide: first, the considerable distance of the rapidly growing, and hence rapidly consuming tip, from the youngest functional polypide; and, secondly, the fact that the tip is separated from that polypide by one or two septæ, whose central cells are highly metamorphosed, and apparently cuticularized, thus serving to break the continuity of the cell wall. An objection to the assumption that the mesodermal cells of the tip derive their nourishment from the products of digestion which have been elaborated by the alimentary tract of the youngest polypides and passed into the body cavity, might be based on the fact that the communication plates are always fully formed between the bud and the next older polypide before the older polypide has become functional. If the communication plate were a closed septum, this would be a fatal objection. But it is not closed to fluids carrying food in solution. The very persistence of an opening indicates that it has a function, and favors the hypothesis here presented.

Positive evidence for the conclusion that the reticulated mesodermal cells take up food material from the body cavity is derived from the fact that these cells often show evidences of being amœboid. Thus they are sometimes found with pseudopodia-like prolongations of the cell body (Figs. 54 and 59). A large percentage of all reticulated cells of this stage show similar appearances. Although they here seem to keep their places in the mesodermal epithelium, their movements being confined to their free surfaces, the cells derived from the homologous layer in marine Bryozoa are migratory. Therefore these may be considered as morphological equivalents of migratory cells, which have come to remain in or have never departed from the mesodermal layer, although possessing some of the characters of these notoriously trophic elements.

That the nutritive matter in the cœlomic cells is supplied to the young bud is what we should expect, since the cells of the bud, being most actively engaged in growth, will require most nutriment. The actively dividing cells of the outer layer of the bud are thick and cuboid, and are rarely so highly vacuolated as the more passive ones of the body wall; yet occasionally one finds one or two huge cells in this layer full of vacuoles, which contain highly refractive bodies. In most cases these cells send out processes into the cœlom, and in a few instances I have seen them united with similar processes from cells on distant parts of the body wall. This remarkable phenomenon, shown in Figure 54 (Plate VI.), may possibly signify that cells of the cœlomic epithelium at times directly communicate with those of the outer layer of the bud to supply it with nourishment. Nutrition of the bud is also probably effected through the presence of large reticulated cells at the angle between the bud and the body wall. A condition like that shown in Figure 56, *cl. ret.*, is very common.

Every author from Dumortier et van Beneden to Braem, who has studied the origin of the polypide in Paludicella, has mentioned the presence of highly refractive bodies in the alimentary tract at the time of its formation. These are very striking in *some* living specimens, and in whole animals after killing. I have found that this highly refractive substance in the bud is exceedingly variable in amount and position, and that sometimes it is apparently absent. When present, it usually occupies the lumen of the forming alimentary canal; but, as sections show, it is often located in large vacuoles in the future digestive cells of the alimentary tract. It seems highly probable that, as Braem suggests, this is nutritive substance, and it has doubtless come from the body cavity through the agency not only of the outer layer of the bud, but also of other parts of the cœlomic epithelium.

I am inclined to interpret the phenomenon of cells filled with nutritive material as an adaptation to the peculiar conditions of Paludicella, in which the individuals are early separated from one another, except for the communication plate, through which at best fluids can pass only slowly, and in which a rapid growth of the body wall to produce the polypide takes place periodically. The mesodermal cells rapidly absorb the nutritive fluids of the body cavity and store them in their substance before the formation of the communication plate, and give them out again during the period of the polypide's most rapid growth chiefly to this part of the individual. This hypothesis has been mainly derived from considering the fact of the great development of the reticulated cells in the lateral bud and the very early completion of its communication plate, the immediate needs of the polypide, which arises only after the formation of the plate, being met by this supply of stored nutriment.[1]

But why is the septum (communication plate) formed so early, if it is desirable for the species that the growing tip should be well nourished by the fluids of the body cavity? Here again I must resort to pure hypothesis. I assume that the early formation of the septum is a provision for the protection of the stock against a rapid influx of the surrounding water in case the branch is broken. One can understand how, if the body wall and growing regions depend upon the fluids of the body cavity for nutrition, an open communication of this cavity with the outside world would be a serious obstacle to regeneration of the body wall in the lost part, or the growth of the stock in any other direction. There is a fact which ought to be mentioned in this connection, as bearing on this hypothesis of the function of the septæ. One frequently finds that in stocks which have been handled with reasonable care the median branches are broken off at either end, and in almost every colony one or more lateral branches are missing from the parent branch. Apparently, then, the lateral branches are unusually subject to destruction, and we find the septæ developed at a much earlier period between them and the ancestral branch than between individuals of the median branch. Compare Plate II. Figure 14, in which the communication plate has not yet begun to form, with Plate VI. Figure 58.

III. Budding in Marine Gymnolæmata.

1. Architecture of the Stock.

I have already described the process of stock-building in Paludicella, and have attempted to show that it follows a certain law. I desire now to present a few observations upon the architecture of certain stocks of marine Gymnolæmata, which will aid in arriving at some general conclusions later on. Other observers have worked out the architectural laws of single species or groups, and I shall refer to their studies either in connection with the species which I have used in common with them, or in the general part of this paper, in considering the process of budding in Bryozoa as a whole.

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[1] Similar conditions to those in Paludicella exist in some marine Bryozoa, and in one of these cases, Bowerbankia, I find them fulfilled by a similar arrangement. The young buds of the stolon which give rise to the "nutritive zoöids" are, at an early stage, loaded with food granules. As in Paludicella, so in Bowerbankia the communication plates are formed early.

I will begin my description with *Bugula turrita*[1] of Verrill, which I gathered in the summer of 1889 at Wood's Holl, where it occurs abundantly on the piles of the wharf. The stock is bushy, and, when its polypides are active, of an orange color. In its simplest form the stock consists of a central axis, which is somewhat zigzag, and gives off lateral branches like the trunk of a tree. The lateral branches are inserted on the trunk in a spiral line. Each lateral branch is fan-shaped (Plate VII. Fig. 64), the part corresponding to the handle of the fan being the point of attachment, and the fans are smaller the nearer they are to the tip of the trunk. The attachment of the branch to the trunk is effected by one primary individual. Each fan-shaped branch extends from its point of attachment obliquely upward and outward, and, although it is slightly concave on its upper inner surface, the concavity is not sufficient to prevent its being spread out upon the slide for study without materially disturbing the interrelation of the individuals in the stock.

I have studied several branches flattened in this way (one of 400 individuals), and have made camera drawings of them. Since the results in the different cases are substantially in agreement, I have concluded that they are significant. One of these camera drawings is shown in the figure just referred to.

To designate individuals in the stock, I have adopted a simple nomenclature. The forty-four terminal individuals are numbered from 1 to 44. The successive generations (if I may be allowed to use this word in a loose way) are indicated by the Roman numerals from I. to XIII. Any one individual is indicated by placing the numbers of the radial line or lines to which it belongs first, and following this by the Roman numeral of the generation to which it belongs. Thus, 27–30 IV. is an individual near the base of the twig 27–30 and of generation IV. Figure 64^a (Plate VII.) is a diagram showing the arrangement of the individuals in Figure 64. The radial lines represent the rows of individuals; the concentric lines separate adjacent individuals of the same radial row. The same nomenclature is used as in Figure 64.

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[1] This species is very similar in general habit to B. avicularia, Linnæus, and to B. turbinata, Alder (Hincks, '80, pp. 75–80). It differs from the first named species by possessing only one spine, on the outer upper edge, as described by Leidy ('55, p. 142), instead of having three, — two outer upper and one inner and upper. It differs from Hincks's diagnosis of the second in having only two "cells" in each branch, instead of 3–6 in the upper portions. The form of the avicularium would seem to ally it more closely to B. avicularia.

In studying Figures 64 and 64^a, one of the first facts which attracts our attention is that (1) *the individuals of the twigs are in pairs, and the adjacent individuals of the two rows "break joints."* In general, one finds that the individuals of the same twig are of the same length; but since the two rows of any twig ultimately rest upon one, either the proximal two individuals of these rows must be of unequal length, or else they must arise on different parts of the individual which supports them. Both of these cases occur. Sometimes one individual (26 IX.) has nearly twice the length of the other (25 IX.), and in other cases (9, 10 VI., 11, 12 VI.) the more proximal of the two individuals (9, 10 VI.) arises so far proximally on the side of the supporting individual 9–12 V. as to have a total length quite equal to that of the more distal (11, 12 VI.). Owing to their different positions upon the individual 9–12 V., these two individuals may be designated as lateral (9, 10 VI.) and terminal (11, 22, VI.). *The terminal individuals continue the ancestral row; the lateral individuals are the first of lateral branches.*

This distinction is an actual, and by no means a meaningless one. The constant difference in position of the two individuals which rest upon one shows conclusively that this branching cannot be regarded as dichotomous, and I may say parenthetically that I shall try to show in the general part of this paper that true dichotomy is not common in Bryozoan stocks, if indeed it exist at all. Now, since in the rows of individuals in which there is no lateral budding the distal lies directly terminal to the proximal individual, that individual which fulfils this condition at the region of bifurcation of the twig must be regarded as continuing the ancestral branch; and that individual, conversely, which arises from the side of the single proximal individual must be regarded as the lateral one. Thus we have the stock composed of ancestral and lateral branches as represented in Figure 64^a.

(2) *When two lateral branches are given off from two ancestral ones which have had a common origin* (and are consequently themselves respectively ancestral and lateral branches), *they are given off towards each other.* This is equally true whether the two lateral branches in question arise in the same generation (32 X., 33 X.) or in different

generations (24 X.', 25 IX.). This may be expressed by saying branches are given off on the side towards the axils.

By consulting Figure 64ª and tracing out the finely dotted lines which connect the second, third, etc. axils of all branches counting from the proximal end of the fan, it will be seen that (3) *lateral buds tend to arise on two closely related branches in the same generation.* There are several slight deviations from this rule. The less closely related the branches, the less marked the tendency, although it is still discernible. (Cf. branches 9–16, 23–30.)

This rule does not hold, however, so well on the margins as in the middle region of the fan, for here another and a superior rule seems to obtain. This is that (4) *lateral budding occurs more frequently at the margins of "fans" than elsewhere.* Thus in Figure 64ª there is at the margins, on the average, 1 case of lateral budding to 4.3 cases of median budding. Elsewhere the average is as 1 to 6.5. In larger fans the difference is even more pronounced. This is true not only for the "fans," but also, to a less degree, for the two "subfans" which arise respectively from the two individuals of generation II. (but 17, 18 is very anomalous in this respect). In general, any rule deduced for the margin of the fans holds true also for subfans to any degree of subdivision; but the less perfectly, the higher the degree.

By consulting again the diagram, it will be seen that the branches have attained different lengths. Thus 9, 10, 29, and 30 contain representatives of generation XIII., while the terminal individual of branch 1 is of generation X., and those of branches 35–44 are of generation XI. So the curve which connects the tips of the branches (see dot-and-dash line, Fig. 64ª) would rise from 1 to 9–10 as a maximum, and fall again till it reached the margin of the first subfan; then rise again, reaching a second maximum in the middle at 29–30, and finally fall again to the other margin. In general, then, (5) *the marginal branches are shortest, the intermediate ones longest,* i. e. *give rise to the greatest number of generations.*

Although the marginal individuals of say generation III., IV., or V. do not support branches with so many generations as the intermediate ones, yet they are not therefore necessarily less prolific in individuals, because the number of branches arising distally of such individuals is greater according to rule 4 than the number arising distally of the intermediate ones. Thus, if we count the number of individuals borne on each of the eight individuals of the fourth (IV.) generation of Figure 64, we find in the given case: —

Outer.	1.	1–8 IV. (an outer individ.)	gives rise to 8 branches	and 34	individ.
	2.	9–12 IV. (an inner ")	" " 4 "	" 27	"
Inner.	3.	13–16 IV. (an inner ")	" " 4 "	" 23	"
	4.	17, 18 IV. (a subouter ")	" " 2 "	" 13	"
Inner.	5.	19–22 IV. (a subouter ")	" " 4 "	" 25	"
	6.	23–26 IV. (an inner ")	" " 4 "	" 23	"
Outer.	7.	27–30 IV. (an inner ")	" " 4 "	" 26	"
	8.	31–44 IV. (an outer ")	" " 14 "	" 56	"

According to the rule that inner branches are slightly prolific, we should expect cases numbered 4 and 5 in the above table to contain the fewest branches and individuals; in accordance with the rule that marginal branches even of subfans are more prolific, we should expect them, on the contrary, to contain more branches and individuals than cases numbered 3, 6, etc. The result is usually a condition intermediate between that of the middle and outer branches, such as is partially realized in case number 5. Case number 4 seems to present an unusual condition, which may be correlated with the fact of its close approximation to number 5. (See Fig. 64, 17–20.) From the consideration of this and other cases, I think this conclusion may fairly be drawn: (6) *Of the four proximal individuals from which a fan arises, the outer two will bear the greater number of individuals, the inner two the lesser.*

Since from rule 2 median individuals (ancestral branches) occupy the margins of fans (or subfans of any degree) and the lateral branches are intermediate, it follows, as a corollary to rule 5, that, in general, the ancestral branches are the shorter, the lateral branches the longer; and, as a corollary to rule 6, that from any axil the ancestral branch will of the two give rise to the greater number of individuals; the lateral branch, conversely, to the less, other conditions being equal.

We have deduced the laws of lateral budding on different parts of the circumference. We find also that there is a regular variation in the frequency of lateral budding, dependent upon the distance of the region from the primary individual of the fan. This rule, like any other, is not invariable, whatever the other conditions may be; but it is more or less dependent upon them. A small and regular fan having seven generations gives this result.

No. of Generation.	Number of Individ.	Increase per Cent.
I.	1	
II.	2	100
III.	4	100
IV.	8	100
V.	12	50
VI.	16	83⅓
VII.	16	0

In this table the first column gives the number of the generation, the second the whole number of individuals in the generation, and the third column the increase per cent of individuals in each succeeding generation over the last. In this specimen the increase underwent a very regular diminution.

With larger colonies so great a regularity as that just shown is hardly to be expected, nor is it found. The following table is based on Figure 64, and is like the preceding; but in addition the percentage increases have been averaged — i. e. the means of successive increases taken in pairs have been given — to eliminate what may be called accidental variations.

Generation.	Number of Individ.	Increase per Cent.	Average.	Generation.	Number of Individ.	Increase per Cent.	Average.
I.	1						29
				VIII.	28	27	
II.	2	100					23
			100	IX.	33	18	
III.	4	100					18
			100	X.	39	18	
IV.	8	100					16
			88	XI.	44	13	
V.	14	75					
			49	XII.	20	Incomplete.	
VI.	17	22					
			26	XIII.	4		
VII.	22	30					

Hence we conclude, *There is a diminution in the rate of increase of individuals in the "fan" as it grows older.*

In searching for an explanation of this phenomenon, I first drew a line from the centre of the primary individual of the fan to the periphery, and divided it into four equal parts. I then described arcs with the primary individual as a centre, and with radii equal to $\frac{1}{4}$, $\frac{2}{4}$, $\frac{3}{4}$, and $\frac{4}{4}$ of this line respectively. Counting the number of individuals cut by these arcs respectively, and dividing those numbers by the length of the corresponding arcs, I found that *there is almost exactly the same number of individuals per unit of arc for each of the four arcs.* (Rule 7.) The previous conclusion, that there is a diminution in the rate of increase of individuals in the fan as it grows older, may then be considered as a corollary to this rule, as it obviously follows from it.

Bugula flabellata, J. V. Thompson.[1] — I have studied this species for the purpose of confirming the results obtained in B. turrita, and have found the architecture of the two species alike in all essentials.

The entire colony of B. flabellata (Plate VII. Fig. 66) may be compared to a single "fan" of B. turrita, only there are usually many more individuals in the former, and of course there is no central stem to which it is attached; but the fan is fastened directly by its rhizoids to the object which supports it.

Usually about four rows of individuals are united, instead of two as in B. turrita, — a condition which can be easily derived from the latter by imagining adjacent branches to become fused together. Here as there adjacent individuals break joints. Here as there lateral branches are given off towards the axils.

Rule 3 is not true for B. flabellata. This is entirely annulled by the establishment of a new rule, which depends upon the new conditions found in this species; namely, that more than two rows cling together, and that consequently one or more rows of individuals are enclosed between outer marginal rows. In any such twig composed of more than two rows (Rule 3a) *lateral branches are given off only from the marginal rows.* (See Fig. 66, 49–54 XVII.) It might possibly result, then, that certain of the middle rows of the twig should never give rise to lateral branches. But I do not believe that this ever occurs in very long rows, for by the splitting up of the twigs the middle rows sooner or later become marginal (so 46–51 XV.). In one stock that I have drawn, consisting of 17 to 21 generations, every middle row occurring as such up to the 13th generation had become at the periphery a marginal row.

As in B. turrita, so in B. flabellata lateral budding occurs most frequently at the margins of fans, — in a fan of about 800 individuals in the ratio of 1 : 10 for the margin, and 1 : 14 for the remainder of the fan. By a comparison of these figures with those given on page 43 for B. turrita, it will also appear that lateral budding is less frequent here relatively to terminal budding than in B. turrita.

The fifth rule deduced for B. turrita holds equally well here. In one case the curve of the tips of the rows rises from the margin of the fan at generation XXIV., reaches 3 maxima of XXVI., XXVII., and XXVIII. respectively, and falls again at the other margin to generation XXIII. In the subfan from which Figure 66 was taken, the curve begins at the outer margin with generation XVII., rises to generation XXII. at two points, and falls again to XX. at the inner margin of the subfan.

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[1] The species which I have studied is identified by Verrill ('73, pp. 711, 389) under this name, and my specimens also agree fairly with Hincks's ('80, pp. 80–82) diagnosis. The two pairs of spines, one longer than the other, could be distinctly seen. Hincks says, "The rows of cells . . . are never, I believe, fewer than four, and range as high as seven." But his Figure 66 shows three rows only in some places.

Of the four proximal individuals in any fan here, as in Bugula turrita, the outermost, ancestral give rise to the greater number of individuals. In one case, for instance, the marginal individuals lie at the base of 31 rows with 184 individuals, while the inner ones support only 7 branches with 65 individuals. Similar results were obtained from other stocks.

With the middle of the primary individual as a centre, I passed an arc of a circle through the extremities of the branches of a large camera drawing of a fan of B. flabellata, divided the radius into eighths, and passed arcs through these points. The number of individuals cut by the different arcs was then counted and tabulated; the arc with the longest radius cut through 87 individuals. By measuring the length of the arcs, the number which should be cut by each arc on the assumption that the number of individuals per unit of arc is constant for all radii was determined. This was then compared with the actual number found, with the following results: —

Length of Radius.	No. of Individuals observed.	Theoretic No.	Length of Radius.	No. of Individuals observed.	Theoretic No.
1	3	2½	5	37	40
2	7	6	6	56	56
3	13	13	7	68	70
4	22	25	8	87	[87]

In this instance, then, the 7th rule deduced for B. turrita evidently holds true for B. flabellata.

While at Mr. Agassiz's laboratory at Newport, during the summer of 1890, I had frequent opportunity to examine other stocks of Bryozoa, which occur there very abundantly. I will take four species as typical examples of the groups they represent, and treat of the architecture of their colonies.

Lepralia Pallasiana, Busk.[1] — It is not at all easy to determine from a young stock what has been the order of succession of individuals. One has to view the object from both sides, make a careful examination of the walls of the zoœcia and of the relation of the polypides to one another, and, when he has done his best to determine what are the facts, he must feel that his conclusions are after all more or less subjective. By a careful study of the colony shown in Figure 71, I have constructed the diagram shown in Figure 71ᵃ.

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[1] I do not feel perfectly certain that the specimen shown in Figure 71 (Plate VIII.) belongs to this species, because the characters of the young stocks differ some-

The stock of Lepralia is a creeping one, and all of its rows of individuals are in juxtaposition. This juxtaposition is continued into the adult stage. Even the young stock begins to show evidence of a quincunx arrangement of individuals. This is less evident in the youngest individuals than in the older part of the stock, and is most evident in old colonies. That there is not here a true dichotomous division of rows of individuals, resulting in the annihilation of the ancestral row and the establishment of two new ones, is evident from a glance at the youngest generation in rows 11, 12, or, better, 2, 3, in which the relation of terminal (11, 3) and lateral (12, 2) individuals is very different. The former continue the ancestral line, the latter establish new rows. Lepralia differs from Bugula in this: that two lateral branches may be given off from the ancestral row in the same generation, as at *B, C,* and *a, a* (enclosed in circles), Figure 71ᵃ.

In contradistinction to the conditions in Bugula, when only one branch arises, it is not given off towards the axil, but away from it.

The synchronism of the budding process noticed in B. turrita is hardly distinguishable in the adult stock of this species; in the young, however, it is quite marked, and gives to the whole a very symmetrical form. The cleavage of eggs does not proceed by more regular steps. Of the three individuals *a, C, a* (in circles), which follow *B,* each has given rise to three others, a median and two lateral. From each of the three individuals derived from the two individuals *a, a* (in circles) has arisen a lateral branch. Rule 3 is therefore well marked in the young stock of Lepralia.

Rule 4, concerning the greater frequency of lateral budding at the margin, is also exemplified in Lepralia. The ratio of cases of lateral to median budding being 1 : 1 on the margin (rows 1–6 and 15–19) and 1 : 2.8 in the middle (rows 7–14.)

In Bugula, as will be recalled, it was concluded that the marginal

what from those of older ones. Yet it is an Escharine closely allied to Lepralia, and I have seen in some cases the broad-based spine on the proximal border referred to by Verrill as being found in L. Pallasiana.

branches were possessed of fewer generations than the intermediate ones. Since by Rule 2 the lateral branches were given off towards the axils, and the ancestral branches therefore always remained marginal, it resulted that the ancestral branches were the shorter, the lateral branches the longer. But in Lepralia lateral branches are turned away from the axils, and here we find the conditions concerning the relative number of generations in marginal and intermediate rows correspondingly reversed. Thus, in Figure 71^a, the terminal individual *D* of row 10, a median but ancestral row, belongs to generation IV. while the lateral branches 6 and 15 have five generations of polypides. Thus it is true here, as in Bugula, that the ancestral branches are the shorter, the lateral branches the longer (page 44).

That the outer individuals *a*, *a*, of rows 6 and 15, have given rise to more individuals than the inner *C*, is clear without further comment. Finally, since the individuals retain a nearly constant width, the necessity of the rule established for Bugula, — viz. that there is almost exactly the same number of individuals per unit of arc for all radii, — and of its corollary, — that the increase of individuals in sucessive generations undergoes a regular diminution, — is apparent.

Flustrella hispida, Fabricius.[1] — This stock is a very dense corm-like one. The primary individual becomes surrounded on all sides by the younger zoœcia. It is very evident from an inspection of the position of this primary polypide with relation to the periphery, that growth occurs most rapidly on each side and in front of the primary polypide. In making any diagram of such a stock, it is not very difficult to decide upon the origin of the more peripheral individuals of the stock, but it is wellnigh impossible to say with any certainty what are the relations of the individuals of the second generation to those of the first. Barrois ('77, pp. 227–229) has, however, determined this for this species, and my diagram (Fig. 67) is based in part upon his observations. I do not desire to insist that the diagram represents the exact method of growth of the stock. It is an attempt to represent it, founded principally on careful study of Figure 69. The quincunx arrangement of individuals is already apparent in the young stock (Fig. 69); it becomes more evident in the adult, and when new individuals arise distad to any two, one of the new ones is median (ancestral branch), the other lateral. (So terminal individual of rows 11 and 10; 22, 23; 43, 44; etc.) In the diagram, however, I have not always indicated which is the median and which the lateral branch, for in the older parts of the colony, owing to a shoving of individuals, it is not easy to distinguish them.

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[1] Hincks ('80, pp. 504–506) makes the existence of a larval bivalve shell a characteristic of this genus, and therefore I assign to it a very common Alcyonidium-like form which was extremely abundant on Fucus at Newport. F. hispida is the only species of this genus. I found the bivalve shell still adhering to the primary individual of a young colony (Plate VIII. Fig. 69, *o*.). In Verrill's ('73, p. 708) catalogue this species is referred to under the name "Alcyonidium hispidum, Smitt."

Lateral branches appear usually to be given off towards the axis. Here, as in Bugula, the lateral branches tend to be longer; the ancestral, shorter.

It is evident from the diagram that lateral budding is most frequent at the margins of the corm, i. e. that part lying posterio-dextral or posterio-sinistral of the primary individual, and that the descendants of the two lateral individuals of the four belonging to generation II. are more numerous than those derived from the middle two. Finally, it is evident that the number of individuals per unit of arc will be the same for arcs of all radii, and therefore the rate of increase of individuals will diminish through successive generations.

In *Crisia eburnea*, Linn.,[1] we find the same laws illustrated. The architecture of the genus has been carefully treated of by Smitt ('65^a, pp. 115–142) as forming the basis of classification. Barrois ('77, pp. 76–85) has described in a masterly way the formation of the young stock of tubuliporid Cyclostomata, and the relationships of the different types of budding in this group. Harmer ('91, pp. 145–173) has recently discussed the architecture of the stock in British species, adopting Smitt's graphic method of showing it. I have found his paper of great value for my purpose.

This species grows as a shrub-like stock upon floating eel-grass, etc. I was wrong in saying, in my Preliminary ('91, p. 282), that Crisia has its branches united in pairs. The comparison of this species made by Barrois ('77, p. 82) with the "geniculata form" is conclusive evidence, to my mind, that the apparent double row is in reality a single one, and that such a branch as 18, Figure 65, is to be represented by a single line in the diagram Figure 65^a. We find here terminal and lateral branches; no true dichotomy. Branches are given off on the side *away* from the axils, as in Lepralia, not as in Bugula. (But branch 11 is an exception to the rule.) They are given off, as Harmer ('91, p. 131) has shown, alternately to the right and left.

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[1] This is the only species of Crisia given by Verrill, and, since my species is very common, it must be the one to which he refers. Moreover, it agrees fairly well with Harmer's diagnosis ('91, p. 131).

There is something of a tendency for lateral branches to be given off in the same generation from closely related branches. Thus (Fig. 65^a) from the primary individual, *o*, of the stock, two individuals, a median and a lateral one, arise. Each gives rise in its first generation to two individuals, a median and a lateral. Of these four individuals each gives rise at the end of three generations of median buds to two buds, a median and a lateral. Comparing 2 and 10, first descendants of the two branches arising from the second individual of 8, we find that each gives rise to lateral branches from their first individual and from their fourth. Comparing 14 and 19, first descendants of the two branches arising from the first individual of 8, we find each giving rise to lateral branches from their first individuals. The law breaks down, however, when an attempt is made to carry it to extremes.

The fourth rule is not always so pronounced in Crisia eburnea as elsewhere, although lateral budding seems to be slightly more frequent at the margin.

The extreme marginal branches usually attain far fewer generations than the more intermediate ones; thus, in Figure 65^a, branch 20 ends in the 7th generation and branch 13 in the 7th also, while the more intermediate branches 15 and 18 attain 12 and 14 generations respectively. So, too, while the outer branches 6 and 1 contain respectively 10 and 11 generations, the inner branches reach 12 and 14.

It is very noticeable that the outer branches give rise to more individuals than the intermediate ones. Figure 65^a will serve to illustrate this also. Here the outer branch 4, the intermediate 8, and the outer 15 possess, together with the branches arising from them, 33, 28, and 40 individuals respectively. Harmer ('91, p. 168) finds this true for his Crisia ramosa, for he says, "It is frequently remarked that the longest and most branched parts of the colony are lateral branches, and not parts of the main stems."

There is, in the long run, a decrement in the rate of increase of individuals in successively older generations, yet it is not so regular a one as that which we found to exist in Bugula. Thus, in the seven generations which even the shortest branches shown in Figure 65^a had attained, the average increase of the number of individuals in the second, third, and fourth generations over the number in the preceding is 67%; in the fifth, sixth, and seventh, 44%. The generations beyond the seventh are not complete; they would have contained more individuals at a later period, when the branches which have now attained only seven generations had grown. Thus the number of individuals in successive generations beyond the seventh increases more and more slowly, and finally decreases to zero. Thus the average rate of increase of individuals in the generations 7 to 10 over those in the preceding is only 16%.

One finds here, as elsewhere, that the number of individuals cut by any unit of arc, the primary individual being taken as a centre, remains practically constant, whatever the radius of the arc.

In studying the creeping stocks of Cheilostomes (Plate VIII. Fig. 71), young corms have been chosen because they exhibit fewer irregularities of formation than old ones. Such irregularities are chiefly due to some unevenness of the surface on which the corms lie, but sometimes apparently to a crowding of individuals. Old rows of individuals are occasionally entirely cut off and end in the middle of the stock; sometimes two rows running side by side, perhaps derived from a common ancestor, suddenly merge into one again. In one case, Escharella variabilis, Verrill, I have seen three rows thus merge into one at the margin, suggesting the existence of a *samknopp* (common bud) in the sense of Smitt ('65, pp. 5–16). Ostroumoff ('86ª, pp. 338, 339) has observed a case in Lepralia Pallasiana. He says: "Dans quelques cas, qu'on peut considérer comme des anomalies, il arrive parfois que deux bourgeons, provenant de loges différentes, viennent à se fusionner." It seems to me, therefore, that while Nitsche ('71, pp. 445, 446), who opposed with such vehemence and success the idea of Smitt that zooecia arise from an undivided marginal zone of cells, was quite right in affirming ('71, p. 447) that even the smallest marginal zooecia are sharply marked off from the adjacent ones, yet he overlooked the possibility that under certain circumstances the lateral walls might fail to develop, and thus one zooecium might arise in the place of two, or even three.

I have not read Smitt's Swedish paper, but I do not find anything in the translation given by Nitsche to warrant the latter's conclusion ('71, p. 446) that Smitt believed the "Gesammtknospe" to be "formed from the sum total of the mature peripheral zooecia." If I understand Smitt, he conceived the *samknopp* not to be derived from the most peripheral mature zooecia, but to be self-proliferating, and to give rise to the rows of zooecia, not to arise from them. It is the "bud of the colony," not the sum of the buds of the peripheral individuals of the stock. In this I would agree with him exactly. Although *usually* one finds the marginal gemmiparous tissue forming the lateral walls at the extreme edge of the corm, and thus apparently separated into wholly distinct adjacent gemmiparous masses; under certain conditions, the lateral wall may not be formed between two or more rows, which will then merge into one.

2. ORIGIN AND DEVELOPMENT OF THE INDIVIDUAL.

My studies on this subject, which were undertaken for the purpose of showing the unity of the type of budding throughout Ectoprocta, have been very fragmentary.

Figure 72 (Plate IX.) has been introduced for the sake of orientation. It represents a longitudinal vertical section through the peripheral part of a stock of Lepralia Pallasiana. The body wall is thicker at the margin (*marg.*), and gradually becomes thinner as one passes backward. A septum (*sep.*) has already arisen cutting off the youngest zoœcium from the more proximal one, which contains a young polypide; proximal to this is another septum, and the distal end of a third zoœcium.

Nitsche ('71, pp. 445–456) has already well described the process of forming the *zoœcium* in Flustra membranacea. In fact, he has studied the organogeny more thoroughly in many respects than I have. Nitsche ('71, p. 452) showed that the wall of the advancing margin of the colony was composed of two layers of cells, — an outer, "Cylinderepithelschicht," which secretes a cuticula, and an inner, "Spindelzellschicht mit anliegenden Körnerhaufen." As the body wall formed directly from these cell layers is left behind by the advance of the margin, it becomes continually thinner. "Die Cylinderepithelzellen der Wandung platten sich weiter nach dem proximalen Ende zu ein wenig ab, besonders die der Unterseite verkürzen sich, die einzelnen Zellen rücken auseinander, die Zellgrenzen werden undeutlicher, die Kerne jedoch bleiben deutlich erkennbar." Vigelius ('84, p. 76) could not find the inner cell layer in Flustra, even at the youngest stages, and consequently he believed that only one existed at the margin, and that this went to form the "*Parenchymgewebe*" of the adult. Ostroumoff ('86^a, p. 336) seems inclined to doubt the existence of any mesodermal *layer* at the distal portion of the budding zoœcium in Cheilostomes, and Seeliger ('90, p. 580) has failed to find in Bugula "eine *zusammenhängende* dem Ectoderm dicht anliegende Schicht von mesodermalen Spindelzellen." Both Ostroumoff and Seeliger, however, believe in the existence of *isolated* mesodermal elements at the budding end.

According to my own observations, there is usually only one continuous layer at the budding margin of the stock. Thus, in Flustrella (Plate IX. Fig. 79) one can usually distinguish a continuous ectoderm, but the mesoderm (*ms'drm.*) is represented by scattered cells only. At the margin in Lepralia (Fig. 73) one finds a thick ectodermal layer, composed of columnar cells, but the mesoderm consists of an irregular thick mass of cells, some of which appear to be amœboid. They however show no signs of having been derived from the outer layer. The condition of the budding margin of Escharella resembles that of Lepralia. In older parts of the body wall, where the ectoderm is reduced to an extremely thin layer, only scattered mesodermal cells appear, and these are amœboid or mesenchymatoid.

On the other hand, one finds in the body wall, around the nascent neck of the polypide (Plate X. Fig. 88), even to a late stage, both ectoderm and mesoderm well formed as *layers*. The ectoderm is a columnar epithelium; the mesoderm is flatter, and often its cells are not sharply delimited from one another. It is thus perfectly evident, to my mind, that the mesoderm has in general lost its original epithelial character in the marine Bryozoa, although it has retained it in Phylactolæmata. Whenever it does exist in the former group as an epithelium, it is at the budding regions (neck of polypide, and Figures 74, 75, 78, 79, *ex.*).

Origin of the Polypide. — There are very few problems in modern morphology, I fancy, the history of whose investigation shows a less satisfactory aspect than that of the origin of the polypide in Gymnolæmata. It is hardly to be wondered, however, that investigators have sought for another interpretation of the process than the most obvious one, because that seemed to oppose many long cherished and wellnigh universally held dogmas. While the first recognition of the animal nature of marine Bryozoa, which we owe to the studies of Bernard de Jussieu in 1742 and John Ellis in 1755, brought with it a knowledge of their colonial nature, yet it was not until much later that the most characteristic part of this process — the formation of the polypide — was clearly observed. Grant ('27, p. 115) and Farre ('37, pp. 400, 409, 415) first described the process by which is formed this complex of organs, and settled once for all the controversy which had sprung up as to whether these animals were truly stock-builders. Under the influence on the one hand of the endosarc theory of Joliet ('77), and on the other hand of the view promulgated by Hatschek ('77), that similar organs in larva and polypide are equivalent as far as regards their origin from the germ layers, the more important papers[1] between '77 and '90 maintained either that the polypide arose independently of the body wall, and secondarily acquired connection with it, or that it had a double origin.

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[1] Excepting those of Barrois, who, from the study of the favorable material presented by metamorphosing larvæ, has persistently maintained the correct interpretation.

To Nitsche ('71, pp. 456–463) belongs the credit of having first described the histological changes in the origin and development of the polypide of marine Bryozoa, particularly with reference to the part which the germ layers play in that process. He says ('71, p. 456): "Die Anlage des Polypids erscheint zunächst als eine Wucherung der Zellschicht der Endocyste in der Mitte der Hinterwand der Knospe, und zwar in dem Winkel, den die Hinterwand mit der oberen Wand macht. Bald ordnen sich die Bestandtheile des regellosen Zellhaufens in zwei deutlich gesonderte Schichten, und wir sehen nun einen rundlichen Körper, bestehend aus einer äusseren einschichtigen Zellschicht, welche sich scharf absetzt gegen die das Innere des Körpers bildenden Zellen."

This stood until a year ago as the most satisfactory description of this process in the adult stock. The appearance within the last year of the two papers of Prouho ('90) and Seeliger ('90) marks a distinct epoch in the advance of our knowledge concerning the origin of the polypide in Gymnolæmata. The paper of Prouho treats of the process in the case of the primary polypide of the metamorphosing larva of Flustrella, that of Seeliger in the case of the young (practically adult) stock of Bugula. According to both authors, the polypide arises from the body wall by an invagination of it, and its two layers are from the first distinct and separate, and go to form the two layers of the adult polypide, and the whole of those two layers. The outer layer of the body wall gives rise to the outer layer of the tentacles and the lining of the alimentary tract, and the inner layer of the body wall gives rise to the mesodermal lining of the polypide. Prouho alone is cognizant of the method of origin of the ganglion, and in addition there are several points of difference between these two authors concerning the development of other organs, to which I shall refer in the proper place. Thus the latest studies have confirmed the assertions of Nitsche, that the polypide arises from a single centre of proliferation of the body wall; they have made an advance in this, that they have shown that the two layers of the bud do not become secondarily differentiated from a single cell mass, but are respectively derived from the two cell layers of the body wall. My own studies have led me to the same conclusion on this point.

Figure 75 (Plate IX.) is a vertical radial section through the margin of an adult Flustrella stock. The ectoderm is relatively thick at the sole (*sol.*) and margin, and very greatly thickened at the point marked *gm.* Here two layers, sharply separated, are apparent. The cells of the outer layer are columnar and full of granular protoplasm, the mesodermal cells cuboid. The body wall has clearly begun to invaginate in this region. Figure 79 is a similar section, and shows a later stage in this process. The lumen of the bud is apparent, and has been formed by invagination, not, as in Paludicella or Phylactolæmata, by ingression. The two layers of the bud are apparent; they have been derived from those of the body wall.

Figure 73 (Plate IX.) shows a stage in the development of the polypide which is intermediate between that of Figures 75 and 79, but from another suborder, Cheilostomata. The mesoderm has here a mesenchymatous character, and is loosely attached to the inner layer of the bud; it is not always sharply marked off from it by boundaries, but is quite distinct in its reaction with staining reagents. This bud has evidently arisen by invagination of the body wall. Seeliger ('90, p. 581) also finds that there is an actual invagination of the ectoderm in Bugula, the opening to which he calls "blastopore."

From what has been already shown, it is evident that in Flustrella, as well as in Cheilostomata, the first appearance of the young polypide is near the margin of the stock, not near the proximal part of the young zoœcium. This will also be apparent at 6 and 9, Figure 71 (Plate VIII.), where the accumulation of nuclei immediately behind the margin indicates the neck of the polypide, — the point at which the bud arose. To be sure, at quite an early stage, but very much later than that of Figure 73, the polypides are found near the proximal wall of the zoœcium, but a delicate funnel-shaped sheath of tissue runs from the polypide to the distal part of the zoœcium, where the polypide is attached to the body wall.

After invagination the pocket closes at its attached end by a growing together of its lips (Figs. 79, 78). Thus the body wall becomes continuous again over the lumen of the bud, and this union is first broken when the fully formed polypide is ready to evaginate itself. Seeliger ('90, p. 582, Taf. XXVI. Figs. 8, 10) has described and figured a similar condition in Bugula.

The young bud now becomes elongated (Fig. 80), the walls of the bud sometimes becoming closely approximated. A little later it begins to pass backwards relatively to the distal wall of the zoœcium. A transverse section through the young polypide and the neck of the colony shows that the connection has become a less intimate one (Fig. 81, *cev. pyd.*). The tissue by which the connection is still effected is that from which the kamptoderm will be formed. It is apparently the existence of this stage, in which the kamptoderm is long drawn out and easily overlooked in optical as well as actual sections, that led to the belief that polypide buds may arise independently of the body wall and only secondarily become connected with it.

At about this time the lumen of the *alimentary tract* begins to be separated from that of the atrium. Thus, in the series from which Figure 81 was taken the more oralward lying sections show that the cavities of the lower and the upper parts of the bud, which at the anal end are broadly confluent, have here become separated by a constriction. A sagittal section of a somewhat later stage is shown in Figure 76, which is from Flustrella. Here we find the alimentary tract represented by a space in the lower part of the bud, broader at its anal than at its oral end and separated from the upper cavity — the common atrio-pharyngeal cavity, *œ.* + *atr.* — by a line of nuclei which represents the line of approximation of the inner layers of the two sides of the bud. The bud is attached to the body wall at its marginal (anal) end, and is free from it oralwards. (Compare with Paludicella, Plate III. Fig. 24.) It seems to me highly probable from these and other series of sections that the alimentary tract is separated from the rest of the lumen of the bud, not by an approximation of the inner layers of the bud along the whole extent of the future alimentary tract at once, but that the rectal part is first formed and constitutes a large cavity, at first broadly open to the atrium above, and that the gastric portion is formed somewhat later by a progressive enlargement of the lower cavity of the bud, which now becomes constricted off from the atrium and œsophagus above. This process is like that found in Paludicella (page 19), which forms a sort of transition to that of Phylactolæmata, described by Braem ('90, pp. 45, 46) and myself ('90, p. 112).

Prouho ('90, p. 448, Fig. 6) shows that the rectum at first appears as a *blind sac* open to the atrium at its posterior end, although later this opening is greatly reduced. Hence in the Flustrella larva also the space from which the lumen of the future rectum is to arise is formed before that of the stomach, although this part of the alimentary tract is the last to be cut off from the atrium. Seeliger ('90, p. 585) says concerning the formation of the alimentary tract in Bugula: "Der ganze Basaltheil des Polypids sich in der Mittelpartie durch zwei immer tiefer werdende Furchen von dem vorderen abschnürt, während er an zwei Stellen, einer oberen und einer unteren, mit ihm in Verbindung bleibt. Die obere Verbindung entspricht dem Anus, die untere dem Mund." The author here seems to imply that the whole alimentary tract is formed at one time; but as he has not attended particularly to this point, this can hardly be said to militate against my view.

There is, however, in my opinion, a more important error in Seeliger's description of the origin of the alimentary tract, — an error into which Nitsche ('71, p. 457) also fell. As in Phylactolæmata and Paludicella, so also in marine Bryozoa in general, so far as I have studied them, the posterior and anterior parts of the alimentary tract are formed independently, and their cavities coalesce only secondarily. The constriction which separates the lumen of the bud into a cavity nearer, "*vorder*," and one more remote from the body wall, "*basal*," does not separate off the whole alimentary tract from the atrium. Neither does that constriction result in the formation of a space opening into the cavity nearer the body wall, "*Vordertheil*," at an upper [distal] point (anus) and lower [proximal] point (mouth). Thus if one examines a complete series of sections through a polypide even of so late a stage as Figure 92 (Plate X.), one finds that, while there is an open connection between the anal end of the alimentary tract and the atrium, the oral end is at all points sharply separated from the cavity above by a double-layered wall of cells, as is shown in Figure 92, between *œ.* and *ga.* Such a condition, moreover, has been found by Barrois ('86, pp. 73–76) in the primary polypide of Lepralia, and by Prouho, as just stated, in the primary polypide of Flustrella.

Origin and Development of the Ring Canal and Tentacles. — Nitsche ('71, p. 430) first described in Flustra a ring canal surrounding the mouth-opening and lying at the base of the tentacles, but did not refer to the origin of it. Seeliger ('90, p. 588) describes it in a young polypide of Bugula, as derived from the mesodermal layer.

My own sections also show that it arises on each side of the œsophagus as a groove lined by mesoderm (Plate X. Fig. 92, right). This canal, which is shown cut along its course in Plate IX. Fig. 82, *can. crc.*, is not wholly separated from the body cavity, but communicates with it below the brain. This communication occurs in the section below that shown in Figure 82, near the point *can. crc.* This ring canal at an earlier stage is shown in Figure 87. It has not yet been formed backwards nearly so far as the brain; anteriorly the section has traversed the tentacles under which it runs. The canal is also shown cut across in Figure 86 at the base of a tentacle, with whose lumen its cavity is directly continuous.

The formation of the tentacles is closely connected with that of the ring canal, from the upper wall of which they arise. Since the upper wall of the ring canal is two-layered, the tentacles are two-layered also. The outer layer of the tentacle is thus derived from the inner layer of the bud; the inner layer, on the contrary, from the outer layer of the bud. It would be hardly necessary to make this statement, which agrees both with early and the most recent observations, had not Barrois ('86, p. 75, Fig. 48) referred to and figured the tentacles as having been formed from the inner layer of the bud *only*.

My observations fully confirm Seeliger's ('90, p. 587) description of the manner of growth of the tentacles; that is, that the outer edge of the ring canal, together with its tentacles, moves downward and outward along the sides of the polypide, turning the axis of the tentacle from a nearly horizontal to a vertical position, and increasing the area of the kamptoderm. Thus in Figure 92 this process has progressed farther on the left side than it has on the right.

Nitsche ('71, p. 458) lays some stress upon the statement that the tentacles are not at first few in number, gradually becoming more numerous; on the contrary, he says, "Ich sah stets, beim ersten Auftreten von Tentakelanlagen, 16, 17, oder 18 Stück gleichtzeitig erscheinen." Seeliger ('90, p. 584) agrees with Nitsche in this respect; but Prouho ('90, p. 449) finds the conditions different in Flustrella. Here the tentacles "ne se développent pas simultanément sur tout son pourtour, mais apparaissent d'abord de chaque côté du plan de symétrie, puis se multiplient vers l'arrière." As I have shown, 14 of the 17 tentacles arise nearly simultaneously in Paludicella, for here there are few of them; and this is the case also in Escharella variabilis with its 17 tentacles.

As the tentacles of both Flustra and Bugula are few in number,[1] the statements may easily be considered to be correct for these genera. The tentacles of Flustrella hispida are much more numerous (30–35), and Prouho's statement may well be true for his form. In fact, my own observations on this species are fully in accord with those of Prouho. Figure 77 (Plate IX.) represents a young polypide of a Flustrella corm, viewed from the roof as an opaque object. Six tentacles were visible on each side of the bud, but the oral and anal parts of the corona were yet incomplete. The remaining nine or ten pairs of tentacles subsequently arise oralward and analward of these rudiments.

Much disagreement has prevailed concerning the number of layers involved in the *kamptoderm* of marine Gymnolæmata, in both the adult and the developmental stages. As in so many other cases, we owe to

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[1] Bugula avicularia has 14 or 15 tentacles, and Flustra (Membranipora) membranacea 20, according to Hincks ('80, pp. 76 and 140).

Nitsche ('71, pp. 431, 432) our first intimate knowledge of this organ. He believed it to consist in the adult of Flustra of a single cell layer, in which are imbedded (or applied?) longitudinal and circular muscle fibres. He believed the kamptoderm to be formed gemmigenetically only by the outer cell layer, the derivative of the mesoderm. Repiachoff ('75, pp. 138, 139) observed in Tendra (Membranipora) "die Doppelschichtigkeit der Tentakelscheide nicht nur bei den jungen Knospe sondern auch bei den ganz ausgewachsenen, offenbar schon längst functionirenden, in ihrem mittleren Theile ganz braunen 'Polypiden,'" and later ('76, p. 152) a similar two-layered condition of the kamptoderm (Tentakelscheide) in Membranipora and Lepralia. Ehlers ('76, p. 37) finds a single layer of cells in the kamptoderm of the adult Hypophorella (Ctenostome), which he believes is continuous with the endocyst of the body wall, and thus is ectodermal. He finds neither longitudinal nor circular muscle fibres. Haddon ('83, p. 517) believes the kamptoderm to be derived from both the inner and outer layer of the polypide bud. Vigelius ('84, pp. 33, 82) describes it as arising from the mesoderm only (Parenchymegewebe), and as being essentially one-layered, both longitudinal and circular muscles lying in this layer. Barrois ('86, p. 74) derives the kamptoderm from the mesodermal layer only. Ostroumoff ('86ª, p. 15) believes the kamptoderm to be two-layered and provided with muscles; it is in his opinion derived from both layers of the bud. Freese ('88, pp. 18, 19) studied only the adult of Membranipora. He admits the presence of muscle fibres, but believes the kamptoderm one-layered. Pergens ('89, p. 507) states only that in the Cheilostomes studied by him the tissue of the kamptoderm is composed "aus abgeplatteten Zellen, zwischen welchen Längs- und Ringmuskelfasern eingebettet sind." Prouho ('90, p. 451) states that in the primary polypide of Flustrella this organ is early differentiated, "et les deux couches de rudiment prennent part à sa formation." Finally, Seeliger ('90, p. 587): "Es kann danach keinem Zweifel unterliegen, dass die Tentakelscheide ektodermalen Ursprungs ist. . . . Das Mesoderm erscheint auf allen gelungenen Schnitten von der Tentakelscheide scharf abgesetzt."

It is my belief that throughout the group of marine Gymnolæmata, as in Paludicella and Phylactolæmata, the kamptoderm is derived from both of the two layers of the polypide bud, is provided with a strong system of longitudinal and a slight one of circular muscles, and contains in the adult two layers, or at least modified representatives of two layers. I have arrived at this conclusion from a careful study by sections of the following genera: Bugula, Lepralia, Escharella, Flustrella, Bowerbankia, and Crisia. The existence of two layers was easily demonstrated in all cases in the young polypide by cross sections of the "neck." The two layers are of nearly the same thickness, and distinctly separated from each other. The presence of two layers in the adult is more difficult to determine, but it was always indicated by the occasional presence of two nuclei lying side by side, and especially at the attachment to the diaphragm. The presence of muscles was demonstrated in all cases (except Bowerbankia, where my few sections did not show the proper region) upon tangential sections of the sheath. I may add, that the existence of muscles is wellnigh conclusive *a priori* evidence of the existence of the mesodermal layer, since nowhere else in Bryozoa, so far as I know, do muscles arise from any other layer. Prouho's evidence in support of his position is perfectly satisfactory to my mind, certainly more so than the negative evidence of Seeliger in support of his. In further support of my statements I may refer to the condition of the kamptoderm (*kmp'drm.*) in Figures 92 and 83, Plate X.

Nervous System. — Since Dumortier discovered, in 1835, a ganglion in Lophopus, there has been seen in marine as well as fresh water Bryozoa a body which has been considered, with greater or less certainty, to constitute the central nervous system. Overlooked by Farre, it was, I believe, first described for marine Gymnolæmata in 1845 by van Beneden, co-worker with Dumortier, for Laguncula (Farrella). Nevertheless, up to the present the evidence of its being a ganglion homologous with that of Phylactolæmata has not been satisfactory. The homology can be established only by determining its similar origin with the brain of Phylactolæmata; its function can be best established by showing the existence of ganglionic cells and fibres. I hope to have advanced our knowledge in both of these directions.

At about the time that the œsophagus and stomach have become confluent, one notices a papilla-like elevation of the floor of the atrio-pharyngeal cavity. This has been noticed by Korotneff ('74) in Paludicella, and by Nitsche ('71, p. 459) and Seeliger ('90, p. 586) in Cheilostomes. It has been called by them "Epistome," and compared with that of Endoprocta or Phylactolæmata. In my own opinion, it is merely a structure brought into prominence by the sinking down of the floor behind it to form the ganglion (Plate X. Fig. 86, *gn.*). This depression has been seen by Barrois ('86, pp. 74, 75) and Prouho ('90, p. 450), and rightly interpreted by them as probably destined to give rise to the central nervous system. That this is the correct interpretation is shown by later stages from different species, as Figures 89 and 83, in which we see the ganglion gradually assuming the position it has in the adult, on the anal side of the pharynx at the base of the anal tentacles.

A section across the pharynx in such a stage as Figure 83 is shown in Figure 87. A comparison with Figure 51 (Plate V.) of my Cristatella paper (Davenport, '90) will show a great similarity of conditions at about the same age, and can leave no doubt concerning the homology of the regions marked in both cases *lu. gm.*; or compare Taf. VIII. Fig. 100, *nh.*, of Braem's ('90) magnificent work. A section through a later stage is shown in Figure 82. The brain has already sent out circumœsophageal nerves, as in Paludicella. The central part of the ganglion does not stain; one sees only a granular mass, sometimes with signs of short fibres. In the cornua (*n'*) one occasionally sees very large clear nuclei with a single nucleolus, lying in the midst of a cell mass which is spindle-shaped and stains more deeply than adjacent cells. These remind one strongly of bipolar ganglionic cells, but fibres could not be traced far from their pointed ends. Series of sections of Flustrella parallel to Figure 82 show, as one passes below the level of the ganglion, a continuous band of cells extending down from it towards the cardiac valve and between the cell layer lining the œsophagus and the surrounding mesoderm. One is reminded of the exactly similar conditions in Paludicella (page 26), and of the "linienartige Zeichnung" seen by Nitsche ('71, p. 431) and Vigelius ('84, p. 42) in the same place in Flustra. These facts go to indicate the existence of a gastric nerve.

At about the time at which the ganglion arises, the cavities of the stomach and the œsophagus become confluent (Fig. 86 *œ.*). At this stage (somewhat earlier than Figure 86) the alimentary tract consists of a U-shaped tube of nearly uniform calibre, and without any indication of the cœcum. The tentacles lie in two parallel rows in the middle of the bud, the corona being incomplete both in front and behind, but less so oralwards than towards the anus (Fig. 77, *atr.*). In fact, while new tentacles are formed later towards the oral median line, they never appear behind the line *atr.* This hinder region has another fate. Its wall increases very greatly in area, diminishes correspondingly in thickness, and forms a large part of the kamptoderm lying behind the post-oral tentacle in Figure 86. With this growth of the kamptoderm the anus is carried backwards, and farther and farther from the posterior ends of the rows of tentacles, immediately behind which it formerly lay.

As the kamptoderm grows in area, the polypide comes to lie in the proximal part of the zoœcium. *Pari passu* with this process occurs the *rotation of the oral tentacles*, as in Paludicella. The oral tentacles which at first lie perpendicular to the roof of the colony (Fig. 86) gradually come to lie parallel with it (Figs. 89 and 83). The œsophagus loses its elongated, laterally compressed form, and becomes circular, and the ganglion lies just below the mouth-opening. Not until now, in fact, can one speak of a mouth. It was not at all formed synchronously with the anus. To illustrate this process I have taken three different genera representing different stages. Similar stages could have been obtained from each genus. By using three genera, the similarities as well as the dissimilarities of the process are indicated. Among other things, the larger size of the polypide and shorter kamptoderm of the Ctenostome Flustrella (Fig. 89) is noticeable.

Lastly, the cœcum is formed as a wholly secondary differentiation of the alimentary tract. This arises in some species relatively earlier than in others; thus it is better developed in Figure 86 than in the later stage of Figure 83.

The lining cells of the alimentary tract now rapidly undergo the differentiations characteristic of the different regions. The most extreme modification takes place in the *pharynx*. In Cheilostomes the cells of this region gradually become vacuolated, until finally very little stainable protoplasma remains. The nucleus lies at the deep end of the cells. A very peculiar modification of the cell walls takes place, in that they become plainly perforated by holes through which the adjacent cells are in communication (Fig. 85). It is in a region similar to this that the cells become cuticularized in Bowerbankia to form the so-called gizzard. The pharyngeo-œsophageal region is also provided with a very powerful musculature of circular muscles (*mu.*, Figs. 85, 86).

Concerning the *origin of the muscles* I have made very few studies. The parieto-vaginal muscles seem to arise, as in Paludicella, from around the neck of the polypide, and the retractors from the oral end of the polypide bud (*mu. ret.*, Fig. 89).

The *neck of the polypide* sinks below the general level of the body wall by an infolding of the latter, as described for Paludicella, and the mass of columnar cells which passes down with it forms, I am confident, the *diaphragma* of Nitsche ('71, p. 432), which is thus exactly comparable with the mass of cells around the atrial opening of Paludicella in Figure 45, *of. atr.* (Plate V.). According to this view, then, the diaphragma is not placed at about the middle of the kamptoderm, but at its proximal end, and all that lies between it and the outer body wall — the non-evaginable portion — has been formed in the elongated neck, exactly as the non-evaginable portion is formed in Phylactolæmata (see

Davenport, '90, Plate IX. Fig. 77, Plate XI. Fig. 98) and Paludicella (Plate V. Figs. 50 and 45).

As my purpose is not so much to present a complete organogeny of Bryozoa as to show the method of origin of the bud and the fate of the layers, I have had to desist from carrying on my studies further in the organography, and have left many interesting and important questions unsolved; such, for instance, as the development and structure of avicularia, the presence of an excretory system, and the degenerative processes which occur with regularity in the polypides.

3. Regeneration of the Polypide.

I have been led to study the regeneration of the polypide because Ostroumoff seems to believe that in regenerating buds the digestive epithelium of the stomach is derived from an extraneous source, — the brown body. Thus he says ('86^a, p. 340) the brown body appears as a cœcal appendage of the young digestive tube. "C'est sur ce dernier [tube digestif] qu'on trouve un groupe de cellules affectant la forme d'un bonnet et se réunissant très tôt à l'angle proximal du rudiment ectodermique. A mesure que les cellules du bonnet, ainsi que la masse brune, sont employées à la formation de la portion moyenne du tube digestif, ces dernières se débarrassent de leur contenu," etc.

The external phenomena of regeneration are well known. In the Membranipora stock, for instance, one sees polypides being produced at the margin, and one finds them older and older as one passes backwards, until finally they are seen to be wholly degenerate, and to be replaced by young polypides. Thus, in passing backward along a single row of individuals in a Membranipora stock about 18 mm. long, I have seen this process of regeneration recurring four times. In Alcyonidiun, too, one finds an apparently regularly recurring degeneration and regeneration of polypides. In the mat-like Cheilostomata the regenerating polypide (Plate VIII. Fig. 71, *pyd. rgn.*) is always found at one place, — namely, on the operculum, — that is, proximal of the opercular opening.[1] In Flustrella it is found in a similar position on the dorsal body wall, proximal of the cuticularized introverted portion. My studies have been chiefly made on the Cheilostomata. Figure 91 (Plate X.) represents an early stage in the formation of a regenerating polypide. Here, as in the marginal polypides, there is a typical invagination involving the two layers of the body wall (*i.*, *ex.*). Owing to the reagent, the body wall is shrunken from its contact with the operculum (*op.*).

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[1] Haddon ('83, pp. 522, 523) has found the regenerating polypide arising from the same place in Flustra membranacea and in Eucratea, and Ostroumoff ('86^a, p 339) in Cheilostomes in general.

If one inquires what has been the histological conditions of this region antecedent to this stage, one must look to younger adjacent and marginal zoœcia, since they reproduce these conditions. I will again call attention to Figure 88, which represents a cross section of the body wall through the region of attachment of the kamptoderm of a young polypide of about the stage of Figure 83. This, then, represents the neck of the polypide, and it is from about this region that the operculum and finally the regenerating polypides will arise. The cells are columnar, and stain deeply about the nuclei, and both cell layers are well developed. Elsewhere in this same individual the body wall is composed of smaller, flatter cells, and two layers are not easily distinguished. The region of the future operculum possesses at an early stage some of the largest, most columnar cells of the body wall. The cells of this region do not, however, retain their peculiarly large size throughout life, but in the adult we find the same region occupied by a flat epithelium, nearly as thin as the epithelium shown in Figure 90. Meanwhile the epithelium of the rest of the body wall has become still more attenuated. The difference between the body wall of the operculum and that of adjacent regions is best shown by the greater abundance of nuclei under the opercular region when the stained stock is looked at *in toto* from the roof (Plate VIII. Fig. 71). The regions of the future opercula are seen, in young zoœcia (Fig. 71, *4*, *6*), to be patches of densely packed nuclei. The opercula of older zoœcia show a slight preponderance of nuclei, and thus indicate more numerous cells. It is from such a region, then, that the young regenerating polypide arises.

As in the case of the marginal polypides, so here, the lips of the invagination pocket close and become fused to form the neck of the polypide (Plate X. Fig. 84). The later stages of the development of the regenerating polypides seem to be the same as those of the marginal buds. Figures 74 and 89 are, indeed, regenerating polypides. I cannot find any evidence that the alimentary tract, or any part of it, is formed in regenerating buds by a method differing in any essential particular from that in marginal buds.

It is well known, however, that the degenerated polypide which forms a "brown body" in the old zoœcium eventually disappears. Haddon ('83, p. 519) maintains that in the developing regenerated polypide "the walls of the stomach, or, more strictly, that portion of the stomach which forms the gastric cœcum, grow round and envelop the brown body, so that the brown body passes as a whole into the alimentary tract of the young Flustra." It seems to me that the burden of proof of such a remarkable occurrence lies with him who asserts its existence, and certainly sufficient evidence is not presented by Haddon.

To settle this question in my own mind, I cut a series of thin sections through a part of a stock of Escharella (which in budding shows a practical identity with Flustra), in which all stages of regenerating polypides were to be found. From complete series, at critical ages, I utterly failed to find any indication of the inclusion *in toto* of the brown mass by the polypide. But I found the alimentary tract of the polypides usually applied to the brown body (*pyd. dgn.*), as shown in Figure 92. At this stage the degenerated mass is surrounded by spindle-shaped cells, and just within these by a homogeneous or lamellated sheath. At later stages the elements of the degenerated mass were seen to be more loosely associated. The cells of the alimentary tract at the same time appear highly granular, and a granular coagulum often partly fills the alimentary tract. Before the new polypide is ready to expand itself, the brown body as such has often wholly disappeared. Just as my sections leave no chance for the brown body to be included *en masse* by the alimentary tract, so too do they yield no evidence of the addition to the latter of new cells from this degenerate mass, as Ostroumoff, in the sentence quoted above, implies.

The interesting facts of degeneration in Bryozoa deserve a more careful study than I have been able to give them. We are quite ignorant of the physiological significance of the regularly recurring degeneration and regeneration in certain Bryozoan colonies. Ostroumoff ('86^a, p. 339) has offered an interesting hypothesis, to the effect that the degeneration of the polypides, the remains of which are taken into the stomach of the regenerated polypide and the undigested portion of which is cast out with the fæces, is a method of excretion, made necessary to these animals from lack of urinary tubules.

IV. Origin of the Gemmiparous Tissue in Phylactolæmata.

After having found that in Paludicella and the marine Bryozoa, as in Phylactolæmata, the growth of the colony takes place at the margin or tips, and that it is here primarily that buds originate, and after having thus found that throughout the group all of the organs of the polypide are derived from two layers, of which the inner gives rise to organs so dissimilar in origin as the central nervous system and the alimentary tract usually are, it becomes a matter of no little importance to solve the two problems, what is the origin of these growing regions, and what that of the two layers. Through the works of Barrois ('86), Ostroumoff ('87), Vigelius ('88), and especially Prouho ('90), on the metamorphosis of the larva and formation of the first polypide of Gymnolæmata we are fairly well acquainted with the facts in this group; but a careful study has not heretofore been made of the Phylactolæmata with reference to the points mentioned above. Korotneff ('89) and Jullien ('90) have published quite extensive papers on the ontogeny of Phylactolæmata, which describe too incompletely the stages which should reveal the required facts.

In order to throw a little light on these questions, I undertook the study of the embryology of two species of Phylactolæmata. But before beginning the account of what I have found, it is necessary to remind the reader of some facts concerning the origin of the polypides in the adult colonies. For our knowledge of these we are chiefly indebted to Braem ('90, pp. 18–32) ; it has also been my privilege to confirm many of them.

The details of the budding process are slightly different in Plumatella and Cristatella. In the latter genus the body wall becomes highly modified as it grows older by the formation of secreted masses which nearly fill most of the ectodermal cells. In Plumatella, on the contrary, the ectodermal cells retain, for the most part, a more primitive, unmodified condition. Here, moreover, by a rapid growth at the neck of the polypides, the individuals are carried to considerable distances from one another, whereas in Cristatella there is a less rapid growth resulting in a compact stock.

In Plumatella, the whole of the embryonic tissue from which any bud arises does not go to the formation of a polypide, but a part of it remains as the neck of the polypide, and gives rise by cell proliferation to the body wall and the *Anlage* of a new bud. Thus the *Anlage* of each bud is part of that of a preceding bud. The question remains yet unsolved, Whence came the *Anlage* of the first polypide? Since the embryonic tissue of the inner layer of the bud, which seems to take the most active part in the formation of the bud, gives rise to both the lining of the alimentary tract and the wall of the brain, it becomes an exceedingly interesting question, From what germ layer is this inner bud layer derived?

In Cristatella, as in Plumatella, not all of the embryonic tissue from which any bud arises goes to form that bud; but some of it is, apparently, passed along under the highly metamorphosed cells of the ectoderm, again to divide itself, one part going to form a new polypide, the other to form the *Anlagen* of new buds. In Cristatella, this embryonic mass of cells of the inner layer of the bud seems to be to a considerable extent independent of the highly metamorphosed ectoderm, and to form at places a sort of third layer, lying below the true ectoderm and above the muscularis with the cœlomic epithelium. Here, too, while it is easy to see buds arise from preceding buds in the adult colony, we cannot consider our question answered until we have discovered the origin of the cells from which, as from a stolon, the *Anlagen* of polypides successively arise.

I desire to say that I have avoided giving a full account of the ontogeny of these species, both because it is not directly required for the solution of the problems in hand, and because we are promised studies in this field by Braem.

The eggs of Phylactolæmata arise, as has long been affirmed, from the cœlomic epithelium of the body wall. The evidence of this is conclusive, for one often sees in a single section various stages in the development of the eggs. (Plate XI. Fig. 93, *ov'*.) It is also to be observed that they do not arise indiscriminately from any region of the body wall, but always close to the neck of a polypide. Sooner or later these eggs, surrounded it may be by a few follicular cells, are enclosed in an oœcium, and here undergo their development up to the stage of a young stock, possessing perhaps a dozen immature polypides. In the figures on Plates XI. and XII. the oœcium (*oœ.*) has been usually drawn, but in Figures 100 and 104 it has been omitted. As a result of cleavage, a blastula is formed, and from one pole of this — *the pole nearest to the neck of the oœcium* — cells are given off which move into the blastocœl (Figs. 94, 98) and finally come to line the cavity. It is important to observe that in the earliest stage of this process found there were four inner cells, of which two are represented in the section (Fig. 94, *ms'drm. + en'drm.*). Thus the two layers of the adult body wall are established. Up to this stage the conditions are practically the same in Cristatella and Plumatella. From now on, they are somewhat different in the two genera.

The first difference to be noticed is in the oœcium itself. In Cristatella the cells composing this rapidly become a pavement epithelium (Fig. 97); in Plumatella, on the contrary, the cells of the oœcium remain columnar (Fig. 99). The neck of the oœcium also differs in the two cases. In Cristatella it is long, thick, and filled with a dense mass of large cells (Figs. 95, *cev. oœ.*, and 101 *, 102 *). In Plumatella (Fig. 99) it is very short.

The second difference concerns the embryo itself, and is connected with the formation of the first polypide. In Plumatella (Fig. 99) the first indication of the formation of the first polypide occurs at or very near the neck of the oœcium, or, since the ingression of cells into the blastocœl took place at the pole of the blastula nearest the neck, we may say near to the pole at which ingression occurred. The cells of the outer layer (*i.*) are elongated and contain large ellipsoidal nuclei which are often pressed close together. All of the cells of the larva stain more deeply at this pole than elsewhere, and those of the inner layer rather more deeply than those of the outer. The nuclei are also very large, those of the outer layer being possibly more prominent than those of the inner; but the difference is not so marked as in the drawing, where too the nucleoli of the inner layer are represented relatively too small. Even at this stage one finds in another section of the same embryo the beginning of a second polypide, whose position is indicated at *. This second polypide is indicated merely by a considerably thickened inner larval layer, and a very slightly thickened outer one. The two polypides are thus seen to be wholly independent of each other. The first invagination further advanced is seen in cross section of the whole larva in Figure 96. The entire outer layer would seem at first sight to be involved in this invagination; but even in this figure there are seen one or two nuclei which lie under the oœcium at the place of invagination. I believe that they will not be involved in it, for at a very little later stage (Fig. 104) one finds a layer of cells lying over the invaginated bud, which I believe are destined to form the ectoderm of the body wall at this place.

Later stages in the development of the larva in this species are not shown. The bud follows, I am confident, the same steps that are pursued by the bud in the adult colony. A placenta-like connection of the larva with the oœcium, which was first described by Korotneff ('87, p. 194), begins at about this stage, and continues until two well formed polypides are present. This "gürtelformige Placenta" begins to form in about the middle of the young embryo, and the elongated cell of the outer layer of the larva, in contact with the oœcium shown on the left of Figure 99 below the *, is, I believe, the first indication of it. The oœcium and larva both continue to increase in size, and the walls of the former become thinner with their increase in area.

The attachment of the oœcium to the body wall of the mother stock always remains small, as in Figure 99, and the embryo, in my experience, does not come in contact with it.

The formation of the first polypide in *Cristatella* is preceded by another process. Just as in the adult colony the inner layer of the polypide does not arise by invagination of the ectoderm, but from the stolonic cells lying at the base of the ectoderm (see Davenport, '90, pp. 108, 109, Figs. 4 and 15), so too in the embryo. The first process then must be the formation of the stolonic cells. Figure 101 shows at the point marked *sto.* (which is at the pole of the embryo whence the inner-layer cells originated) that certain of the cells of the ectoderm appear to be arching over a disk, containing about six cells in section, and thus coming in contact with the cylinder of cells (*) which projects from the neck of the oœcium. By a continuation of this process, the central disk of cells gradually comes to lie below the general level of the ectoderm, and to be cut off from contact with the neck of the oœcium (Fig. 97, *sto.*). The position of the stolonic mass with reference to the neck of the polypide in this last figure must be considered abnormal; it is at any rate exceptional, as it lies at one side of the neck of the oœcium, which does not, therefore, appear in this section. The next later stage which I have found is shown in Figure 102. The stolonic mass seen lying beneath the ectoderm in Figure 97 has here already given rise to a young polypide (*i.*, *ex.*), and its area is increasing in all directions by cell division (*sto.*). The beginning of a second polypide is indicated on the right at *sto.* The ectoderm is seen lying above this stolonic mass, and closely applied to the neck of the oœcium (*).

Neither at this nor at any subsequent stage have I been able to detect in Cristatella any "gürtelformige Placenta" such as exists in Plumatella. I am therefore of opinion that the process of nutrition, which is effected in Plumatella from the oœcium through its placenta, is effected in the Cristatella larva by its attachment to the neck of the oœcium. I am pleased to see that Jullien ('90, pp. 13, 14) has also reached this conclusion in a paper which he has had the kindness to send me. At a later stage, the embryo, or young colony, seems to become detached from its intimate association with the neck of the oœcium, as we see in Figures 95 and 103.

Figure 103 represents a stage in which there are two well developed buds, both shown in the section. There is, in addition, on another section, one less developed. The stolon is seen passing oralward of these two primary polypides, or rather the primary and secondary one. Moreover, as the series of sections shows, the stolon does not exist merely in this section, but it is a disk which is cut here in one of its diameters. A separation of the stolonic mass has occurred between the two oldest polypides, so that the ectoderm is here in contact with the cœlomic epithelium, just as is the case between buds in the adult stock. As the colony increases, the inner and outer margins of the stolonic tissue continue to extend farther outward, and this tissue forms at first a broad ring of ever increasing diameter. Later, as the area of the stock increases, the ring becomes broken, so that, instead of growing along an infinite number of radii, its growth is confined to a few, as in the adult colony.

I will defer a discussion of the significance of these facts to the general part of this paper.

B. GENERAL CONSIDERATIONS.

I. Laws of Budding.

Carefully conducted studies on stock building have generally revealed, just as these on Bryozoa have shown, a law in budding. This law in budding results in the formation of a stock the interrelation of whose individuals is a determinate one. I now propose to offer an hypothesis to account for the existence of these laws, and then to show how facts of budding in Bryozoa and other groups can be explained by means of it.

And first of all I must acknowledge that this hypothesis, although perhaps here first formulated, really depends upon observations and deductions made long ago on this group, first by Hatschek, who from 1877 has maintained that individuals do not arise independently of one another, and secondly and mostly to Braem, who in '88 (pp. 505, 506) declared of Phylactolæmata "dass in dem Stock keine Knospe entsteht, die nicht auf das embryonale, d. h. den specifischen Leistungen der Körperwand noch nicht angepasste Zellmaterial einer älteren Knospenanlage zurückgienge und dass somit in der ersten Knospe des keimenden Statoblasten sämmtliche Knospen des künftigen Stockes implicite enthalten sind." Not less is the following hypothesis indebted to the ideas of Roux and Fraisse, and to Nussbaum, who has said ('87, p. 293): "Ein lebendes Wesen ist somit als Ganzes oder in seinen Theilen soweit individualisirt und vergänglich, als die Gewebebildung und die Theilung der Arbeit vorgeschritten ist; das Ueberdauern der Einzelexistenz, die Theilbarkeit auf geschlechtlichem oder ungeschlechtlichem Wege, spontan oder künstlich bedingt, ist an das Vorhandensein undifferenzirter Zellen gebunden und ist um so grösser, je weiter im Organismus diese Zellen verbreitet sind"; and, finally, to the idea which is implied in the conclusions of Nussbaum ('80, pp. 106–113) and Weismann, that germplasma does not find its origin in the parent individuals, but is merely borne by them in its unbroken passage from generation to generation.

This hypothesis is simply that *there is in every stock of Bryozoa a mass of indifferent cell material which is derived directly from indifferent cells of the larva or embryo, and whose function is to form the organs of the various individuals, including the polypides.* This indifferent cell material lies in the body wall, principally at the growing tip or margin of the stock. By its growth and differentiation it gives rise to the body wall, muscles, etc., and at intervals it leaves behind, as a portion detached from itself, a mass of indifferent cells, which is capable of forming a polypide, or of becoming a new centre of growth, or of both. Which of these possibilities will be fulfilled, where and when these masses of indifferent cells will be left behind, depends upon the necessities of the species, and the variations in these respects give rise to the peculiar characters of the different stocks.

This hypothesis differs from that of Braem in that the pre-existence of a *Knospenanlage* assumed by Braem is, according to my view, a non-essential feature in the formation of the colony; the pre-existence of an indifferent cell mass, which does not itself constitute buds, but may give rise to masses which can, is the only essential feature.

As a first application of this hypothesis I refer the reader to the conditions of stock formation in *Paludicella*, already described. We find at the tip of the colony a mass of large proliferating cells, which I regard as histologically undifferentiated. These cells give rise to the body wall, — the cystid, — and at intervals leave behind three masses of cells, which I regard, from the fact that they retain their cuboid condition, as well as from their ultimate fate, as indifferent or embryonic. The median mass of each of these gives rise to a polypide, and to one only. The lateral masses form centres of growth similar to the one from which they were derived.

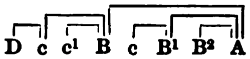
In order to reproduce the arrangement of individuals in the stock resulting from this manner of budding, we may make use of some graphic method of representation, as Smitt ('65ᵃ, pp. 139, 140) did long ago, and as Allman ('70), Semper ('77, pp. 67–78), Chun ('88, pp. 1167–1180), Braem ('90, pp. 33 and 44), Ehlers ('90, p. 9), and others, have since done. I shall represent the mass of indifferent cells by an asterisk, and individuals (according to Chun's nomenclature) by the use of the large and small letters of the Roman alphabet, and, finally, by Greek letters. The typical stock of *Paludicella* might then be graphically represented thus (cf. Plate I. Figs. 2 and 2ᵃ) : —

```
                                                  *
                                                * c *
                                                *   *
                                              * a b a *
                                    *           *   *
                                  * b *       * *   * *
                                  *   *     * β a a a β *
                       *        * a a a *     * *   * *
             *       * a *        *   *
(1)        * D         C            B               A
             *       * a *        *   *
                       *        * a a a *     * *   * *
                                  *   *     * β a a a β *
                                  * b *       * *   * *
                                    *           *   *
                                              * a b a *
                                                *   *
                                                * c *
                                                  *
```

Here the letters indicate polypides or their *Anlagen*, and the asterisks indifferent tissue. The individuals represented by capital letters may be called primary individuals; they may be said to belong to the primary series, and to have been derived from the primary indifferent mass. The individuals represented by small Roman letters will then be secondary individuals, belonging to the secondary series and arising from secondary masses, etc. It is to be observed that this indifferent tissue is here found only at the tips of branches or *Anlage* of such. No asterisks are found adjacent to the adult polypides A, B, C, etc., which have given rise to lateral branches, and these have therefore no power of producing new parts of the colony. The asterisks must not be regarded as having been descended from the letters which they adjoin, but from the terminal asterisks only; that is to say, in Paludicella embryonic tissue has originated from terminal embryonic tissue, and not from indifferent tissue left remaining alongside of the polypides.

Conditions differing in an interesting manner from these were found by Braem ('90, pp. 18–32) and myself (Davenport, '90, pp. 103–106) in Phylactolæmata. In *Plumatella* Braem has shown in the clearest manner how some of the embryonic tissue around a polypide at the proximal end of a nascent branch is carried away to the oral side of the "mother polypide," and lays the foundations of another polypide. In like manner the embryonic tissue around the "mother polypide" may give rise to one or several additional embryonic masses. He has also (pp. 29–32) shown in the most convincing way that each mass, particularly in the case of secondary buds, consists of two parts, of which one goes to form the polypide; the other contributes to the further growth of the common cystid and the formation of new embryonic masses. Since here every embryonic mass is in intimate relation with a polypide, and since the polypides arise nearly in one plane, only secondarily moving out from it, the relation of individuals may be expressed by a formula occupying a single line. Braem has thus expressed it: —

(2)



According to the system adopted for Paludicella, this may be given thus: —

$$\ast\alpha \quad \ast\mathrm{a} \quad \ast\mathrm{b} \quad \ast\mathrm{A} \quad \ast\mathrm{a} \quad \ast\mathrm{B} \quad \ast\mathrm{C}\;\text{✱} \tag{3}$$

or, more developed, thus: —

$$\ast\alpha_1 \quad \ast\alpha \quad \ast\beta \quad \ast\mathrm{a} \quad \ast\alpha \quad \ast\mathrm{b} \quad \ast\mathrm{c} \quad \ast\mathrm{A} \qquad \ast\alpha \quad \ast\mathrm{a} \quad \ast\mathrm{b} \quad \ast\mathrm{B} \quad \ast\mathrm{a}\,\ast\;\mathrm{C} \quad \ast\mathrm{D}\;\text{✱} \tag{4}$$

in both of which the right hand asterisk (✱) takes the place of the A at the right of Braem's diagram. These symbols denote that we have a mass of indifferent tissue connected with each polypide, or the *Anlage* of such; and this indifferent mass, as well as the adjacent polypide, was derived from some other indifferent mass. Thus the masses connected with A, B, C, D are to be regarded as having been cut off from the embryonic mass at the extreme right; and each of these secondarily gives rise to the polypide buds a, b, etc., and their embryonic tissue. Thus we have to do with centrifugal budding only.

In *Cristatella* the conditions are essentially similar to those in Plumatella, the chief difference being that usually only two polypides with their embryonic masses arise from each polypide. This condition may be represented by the formula: —

$$\ast\alpha_1 \quad \ast\mathrm{a} \quad \ast\beta \quad \ast\mathrm{a} \quad \ast\alpha \quad \ast\mathrm{b} \quad [\ast]\mathrm{A} \quad \ast\alpha \quad \ast\mathrm{a} \quad \ast\mathrm{b} \quad [\ast]\mathrm{B} \qquad [\text{✱}] \tag{5}$$

in which the embryonic masses originally attached to A, B, etc., are bracketed to indicate that they are normally no longer active in giving rise to new polypides. As a matter of fact, the secondary rows often make a greater or less angle with the primary ones, and as a result lateral branches are formed. Taking this character into account, the Cristatella formula might be written: —

$$\begin{array}{cccccccccc}
 & & & & & & & & & \ast \\
 & & & & & & & \ast & & \mathrm{b} \\
 & & & & \ast\alpha_1 & & — & \alpha & & | \\
 & & & & & & & | & & [\ast] \\
 & & \ast\beta & & — & & & \ast\mathrm{a} & — & \mathrm{A} \\
 & & & & & & & & & | \\
\ast\mathrm{b} & & — & & & [\ast]\mathrm{B} & & & — & [\ast] \\
 & & & & & | & & & & \\
 & \ast\alpha & & — & & \mathrm{a} & & & & \\
 & & & & & \ast & & & &
\end{array} \tag{6}$$

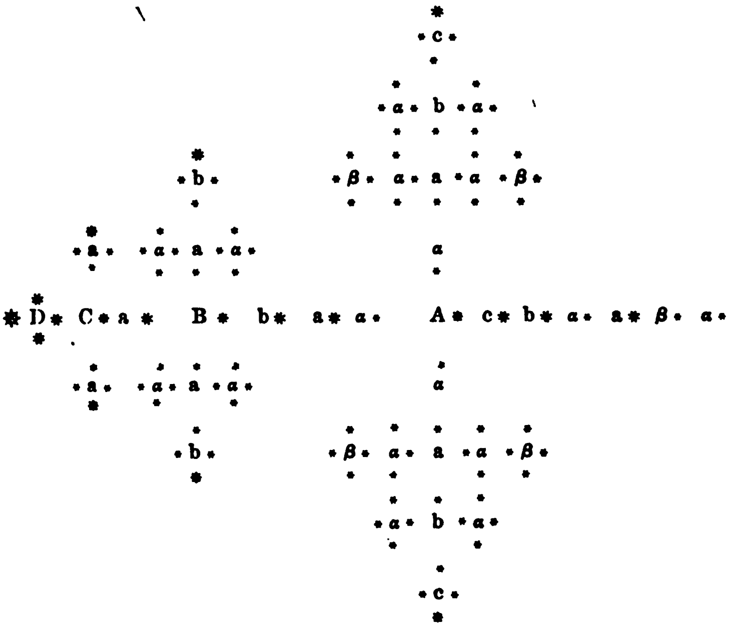
This representation indicates the fact that the first formed buds (A, a, α, etc.) are lateral ones; the second, median (Davenport, '90, p. 106). Intermediate stages between the condition in Plumatella, in which an indefinite number of polypides and gemmiparous masses can be budded off from pre-existing gemmiparous masses, and the condition in Cristatella, in which only two such arise, occur apparently in some species of Plumatella, in which, as Braem ('90, p. 31) has shown, few polypides are produced from any gemmiparous mass, and all but two of these generally do not develop. In the young corms of Cristatella, on the other hand, more than two polypides may thus arise.

Other *Ctenostomata* show a regularity in the budding process similar to that of Paludicella, and exhibit instructive variations upon it.

Victorella, an interesting Ctenostome occurring in slightly brackish water, and first described by Kent ('70) in 1870, possesses, according to the pregnant observations of Kraepelin ('87, pp. 75, 76, 154–157), a stolon-like tube, from which at intervals polypide-bearing "cylindrical cells" arise. Kraepelin ('87, pp. 155–159) has shown it to be in the highest degree probable that the protrusion of the body wall in the neck region of the polypide of Paludicella is the homologue of the "cylindrical cells" of Victorella, and that the remainder of the zoœcia of Paludicella is homologous with the "stolon" of Victorella. While in Victorella the cylindrical cell is developed to such an extent that the retracted polypide is still included within it, and the stolon remains of small calibre, in Paludicella, owing to its shortening, the retracted polypide must seek refuge in the stolon, whose diameter is consequently increased to receive it. Evidence for this is found in the stolon-like nature of the youngest zoœcia of a hatching winter bud of Paludicella Ehrenbergii, and in the elongated cylindrical cell of the adult Paludicella Mülleri, Kraepelin, which must be considered a form intermediate between P. Ehrenbergii and Victorella.

The architecture of the Victorella and Paludicella stocks is, then, similar, in that they both consist of a row of individuals successively formed at a stolonic tip. The resemblance is heightened by the fact that, as in Paludicella, so also in Victorella, a pair of lateral buds is given off from each zoœcium to form lateral branches (Kraepelin, '87, p. 157). As in Paludicella, so also in Victorella, communication plates, *Rosettenplatten*, arise early to separate the zoœcia from each other. But Victorella differs from Paludicella in this, that while in the latter the neck of the polypide does not become the centre of origin of new buds, in the former it does, just as is the case in Plumatella (Kraepelin, '87, Plate III. Fig. 75); that is to say, there are laid down from the tip of the branch three masses of bud-producing tissue, besides that which goes to form the polypides of the primary branch. The graphic representation of this species will therefore be more complicated than that of Paludicella, and has this form: —

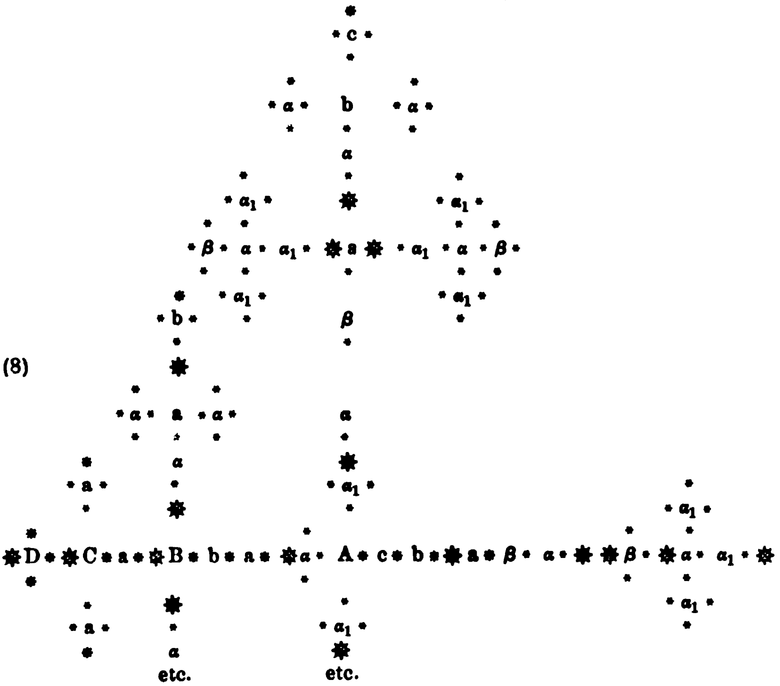
(7)



Compare with (1), page 73, and (4), page 74.

From around each individual of the series A, B, C, etc., which has been derived from the tissue of the stolon tip, there arise series of lateral and of median buds. From around each of the lateral buds, in like manner, both lateral and median buds of a higher order arise. But from each of the median buds only median buds arise. These median buds, are not, however, all of the same kind. The one first produced (a ✱, of Formula 7, ✸ of Form. 8) differs from all formed after it (b ✱, c ✱, d ✱, etc.) in this, that it bears no polypide, but forms the tip of a stolon from which both median and lateral buds arise (β, α, near extreme right of Form. 8). From the second and all succeeding median buds (a b, c, etc., Form. 8), there arise only median buds of a still higher order. Of the latter, the first, as before, produces no polypide, but becomes the tip of a stolon giving rise to both median and lateral buds; the others give rise to only median buds of a still higher order, and so on. Our former formula assumed that all median buds were alike, and all incapable of giving rise to lateral individuals. Their dissimilarity introduces a complication, so that the species must be represented by some such formula as this[1]: —

(8)



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[1] It must be borne in mind that such a graphic representation as this, while it agrees with the descriptions and figures of Kraepelin and Hincks ('80, Plate 79) so

in which the heavy asterisks represent the budding tips of the stock, which give rise to new individuals (tips of the stolons), and α_1, β_1, etc. indicate individuals of the fourth order. The lighter asterisks indicate, as before, points of proliferation from which new buds may arise.

It seems highly probable that Victorella finds near allies in Mimosella and other genera of the Stolonifera.

In *Hypophorella expansa*, according to Ehlers ('76, pp. 5–9) and Joyeux-Laffuie ('88, pp. 137–139), the stolon is composed (as in Victorella), of a number of internodes, each separated from the other by communication plates, and bearing on the distal end typically a feeding zoöid (Nährthier) and a lateral stolon. It seems to me that the jointed condition of the stolon is reasonably accounted for in the same way as that of Victorella, by supposing that each internode, together with its zoœcium, is comparable with the whole indvidual of Paludicella. The "feeding zoöids" of Hypophorella will then be comparable with the *Cylinderzelle* of Victorella. Two facts are opposed to this view: first, the polypide is not formed primarily in the stolon, coming only secondarily to lie in the *Cylinderzelle* as in Victorella; and, secondly, there is a *Rosettenplatte* in Hypophorella between the feeding zoöid and the stolon, while none exists in Victorella. But upon this assumption one can best account for the fact that the stolon is composed of as many joints as there are feeding zoöids, — a condition which appears to occur in only a few other genera, and these closely allied to Victorella. Thus, in Cylindrœcium pusillum and C. dilatatum of Hincks we have two species which may be considered to represent two possible intermediate stages between Victorella and Hypophorella, not only on account of the jointed stolon, but also on account of the enlarged distal end of the joint, which is eminently characteristic of the allies of Victorella. The first objection, that the polypide is not developed in the stolon, but first arises in the well formed zoœcium of the feeding zoöid, might result from the increased importance of the zoœcium over the *Cylinderzelle.* The formation of the plate between the zoœcium and the stolon might be accounted for by the physiological need of such an organ resulting from the increased importance of the zoœcium (cf. p. 40). Such plates exist, in fact, between the primary median individuals, and those secondary median ones in Victorella which are budded from the *Cylinderzelle.* This hypothesis

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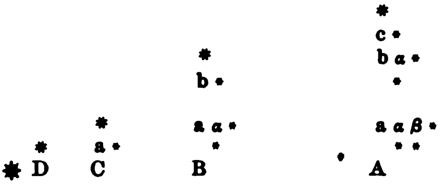
far as they go, may not fit the conditions in all parts of the colony. Moreover, it is to a certain degree idealized, i. e. subjective, for even in the figure of Kraepelin ('87, Fig. 75) one of the individuals of the series a, b, c, etc. has given rise to no stolon as its first bud.

is further supported by the fact that, as a stolon may arise from the *Cylinderzelle* of Victorella, so in Hypophorella such a condition is not uncommon, although hardly typical. In accordance with this hypothesis the formula for Hypophorella might be given thus: —

(9)



$$\begin{array}{cccc}
 & & & \ast \\
 & & & c\,\bullet \\
 & & \ast & b\,\alpha\,\bullet \\
 & & b\,\bullet & \bullet \\
 & \ast & a\,\alpha\,\bullet & a\,\alpha\,\beta\,\bullet \\
\ast & a\,\bullet & \bullet & \bullet\,\bullet \\
\ast\,D & C & B & A
\end{array}$$

Ehlers ('76, pp. 127, 128), in founding the group of Stolonifera, classified the different methods of arrangement of the individuals in the colony as follows: —

- I. Many polypides (*Nährthiere*) on the single joints of the stolon (*Stengelgliedern*).
  - 1. On the entire length of the joints.
    - (a.) Arranged in two rows.
    - (b.) Arranged in a spiral.
    - (c.) Arranged in one row.
  - 2. At the ends of the joints.
    - (a.) In rows.
    - (b.) Massed.
- II. Only one polypide *Nährthier* on a joint of the stolon.
  - 1. Polypide lateral, near it one or many stolonic joints (Hypophorella).
  - 2. Polypide terminal.

In the present state of our knowledge, it is very difficult to say how the types of budding shown in those Stolonifera which possess more than one *Nährthier* on a joint of the stolon are related to, or are to be connected with, the types of Paludicella, Victorella, Hypophorella, or other genera possessing only one *Nährthier* to a joint. This could doubtless be determined, however, by studying the early stages in the development of the stocks. Taking them as they are, however, we find a very simple condition in the stocks of Class I., in which the *Nährthiere* are arranged in a single row, as in *Vesicularia spinosa* (cf. Hincks, '80, Plate 73, Figs. 3–7). The tip of the stolon consists, as I have myself observed in allied species, of somewhat cubical cells of variable thickness, and it is from this tip that the *Anlagen* of the individuals arise. Lateral branches occasionally replace a *Nährthier*, and the latter seems never to produce secondary individuals. The formula of the stock might be written: —

$$(10)\qquad \begin{array}{cccccccccccccccc} & & & & & & & & & & & & & \ast & & \\ & & & & & & & & & & & & & b & & \\ & & & & & & & & & & & & & a & & \\ \ast & F & - & E & - & | & - & D & - & C & - & B & - & | & - & A \\ & & & & & a & & & & & & & & & & \\ & & & & & \ast & & & & & & & & & & \end{array}$$

In *Bowerbankia pustulosa* we have two rows of individuals produced side by side from near the end of the stolon. This condition would be represented by

$$(11)\qquad \begin{array}{ccccc} \ast & \ast D & \ast C & \ast B & \ast A \\ \ast & \ast D & \ast C & \ast B & \ast A \end{array}$$

provided the individuals of this primary series possess the power of giving rise occasionally to secondary buds, as seems certainly to be the case in some members of this genus which I have seen. The spiral arrangement of some colonies is striking; it is of evident advantage to the stock, but its cause in these cases is wholly unknown.

In every one of these cases, and, in fact, in all of those figured by Hincks, which belong to the Stolonifera, there is no trace of dichotomy. Throughout we have to do with linear series, which give rise to lateral branches.

Turning now from the Stolonifera to the other grand division of Ctenostomata, the *Alcyoniidæ*, we find the same prevalence of a law in budding. In its typical expression it may be written as follows: —

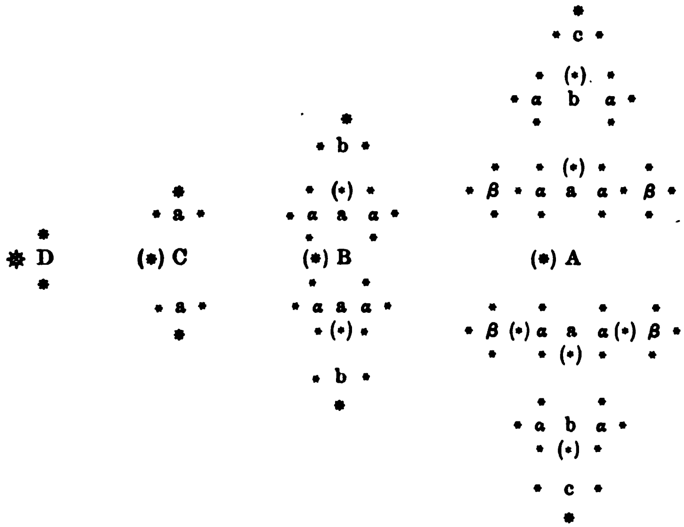
$$(12)\qquad \begin{array}{ccc} & & \ast \\ & & \ast\ b\ \ast \\ & \ast & \ast\ (\ast)\ \ast \\ & \ast\ a\ \ast & \ast\ a\ a\ a\ \ast \\ \ast & & \ast\qquad\ast \\ \ast\ C & (\ast)\ B & (\ast)\ A \\ \ast & & \ast\qquad\ast \\ & \ast\ a\ \ast & \ast\ a\ a\ a\ \ast \\ & \ast & \ast\ (\ast)\ \ast \\ & & \ast\ b\ \ast \\ & & \ast \end{array}$$

Although secondary median individuals are not habitually formed, yet, owing to the capacity of regeneration possessed by individuals A, B, C, etc., an asterisk is affixed in parentheses to show the probable persistence of embryonic tissue. Of the lateral series one or both may fail to be developed.

It might be difficult to determine whether in this group we have to do with dichotomy, did not the tips of the margins at times reveal the fact that there is no division of the ancestral series, but that a new one is added at the side of an ancestral one (Plate VIII. Fig. 69), where of the marginal individuals 4 is clearly median (ancestral) and 3 is lateral, 13 median and 12 lateral, etc. (see page 49).

The members of the group of *Cyclostomata* seem to be closely related, and the method of budding is so similar throughout the group that it seems fair to interpret the more compact Tubuliporidæ from the Crisiadæ. In *Crisia*, as we have seen, individuals are placed in rows, from which at intervals lateral rows are given off to the right or left. One may say that typically these are given off from each individual to both the right and the left, although in some cases, as in Figure 65ᵃ, lateral branches are typically given off alternately to the right and left, and are often aborted. Perhaps the most general formula of all for Cyclostomes should be that of two lateral branches from each individual, one or both of which may remain undeveloped. Such a formula I believe to be also the typical one for *Bugula* and its allies, and for the *Flustrina* and *Escharina*. It would be written thus: —

(13)



in which the parenthesized asterisks indicate the presence of regenerative tissue. This is identical with (12) and similar to (1).

Braem ('90, pp. 130–133) has already called attention to the difference between Phylactolæmata and Gymnolæmata in the *orientation of the* *polypide.* In Phylactolæmata the oral aspect of the polypide is turned towards the margin of the corm or the tip of the branching stock; in Gymnolæmata, on the contrary, the anal aspect is turned in that direction. This difference is a very striking and constant one. It is correlated with another difference in the law of budding of the stock, which will become evident upon comparing Formulas (4) and (5) on page 74, of Phylactolæmata, with Formulas (1) on page 73 and (7) to (13). In all of these the margin or tip of the stock is at the left, the centre at the right. In the formulæ of Phylactolæmata the budding is *centrifugal,* new individuals being produced from the embryonic masses towards the margin; in the formulæ of Gymnolæmata budding is *centripetal,* new individuals being produced from the embryonic masses towards the centre. *In both Phylactolæmata and Gymnolæmata the anal aspect is turned towards the gemmiferous region.*

Braem calls attention to one other difference, namely, that, in the case of the retracted polypide, in Paludicella the rectum lies next the attached surface of the stock; in Phylactolæmata, the œsophagus. A mechanical cause of this is suggested when this statement is put in other words: the polypide in its retracted position is stored in both Phylactolæmata and Gymnolæmata proximad of the atrial opening; i. e. away from the tip or margin, and towards the centre of the stock. May not this be explained, in part at least, as an adaptation to room?

I will here add four examples of regular budding taken from other groups of animals, to illustrate the general applicability of this method of representation. The first of these is that of the Siphonophore *Halistemma* whose formula has been worked out by Chun ('88, p. 1169), and expanded and illustrated by Korschelt und Heider in their recent textbook (p. 39). It runs as follows: —

(14) D c b a C d c b a B e d c b α a γ β α A

According to my interpretation of the case, this formula might be written (15): —

✹D ✹c *b *a *C ✹d *c *b *a *B ✹ *e *d *c *b *α *a *γ *β *α *A,

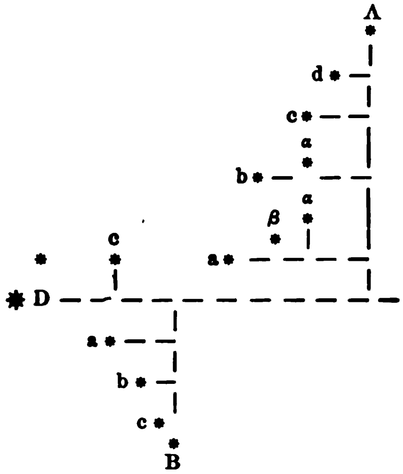
in which the ✹ behind B has been derived from the embryonic mass at A, that behind C from B., etc. The ✹'s represent embryonic masses from which a, b, c, etc. are derived.

If we assume that the terminal individual (A) has not been derived from the primary embryonic mass, at the extreme left, but has had its origin in the embryo, the formula would have to be written somewhat differently; namely, thus (16): —

✸ C ✸ c✱ b✱ a✱ B ✸ d✱ c✱ b✱ a✱ A ✸ e✱ d✱ c✱ b✱ α✱ a✱ γ✱ β✱ α✱ [A]

In a species of *Pennaria*, common on our coast, which is probably Pennaria tiarella, McCready,[1] I have noticed the presence of a similar law of budding. The whole stock lies in one plane, the lateral branches arising alternately from the right and left of a central stock, like the barbs of a feather. These lateral branches give rise to a series of secondary ones, which are all placed on the same (axial) side of the branch. Each branch, of whatever degree, originates as a bud bearing a polyp. From the elongating stalk of this terminal polyp, buds arise, — the beginnings of branches of the next higher order. The stock may be represented by the following formula: —

(17)



Expressed in a linear series, this formula may be written: —

(18) ✸ D✱ C✱ B✱ c✱ b✱ a✱ A✱ d✱ c✱ b✱ α✱ a✱ β✱ α✱

which is identical in form with the second formula (16) given for Halistemma.

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[1] This species is figured by Leidy ('55, Plate 10, Figs. 1–5) and Verrill ('73, Plate XXXVII. Fig. 277). An allied species, P. gibbosa, is figured by Louis Agassiz in the "Contributions" (Vol. III., Plate XV. Fig. 1). In describing P. Carolinii, Weismann (Entstehung der Sexualzellen, p. 122) says that the lateral hydranths do not possess the capacity of giving rise to new lateral hydranth-buds (of a higher order). But, as indicated above, P. tiarella seems to do this regularly. Leidy's and Verrill's figures show the same thing.

Lastly, this formula may be applied to certain cases of fission, as in *fresh water Annelids.* As is well known, the fissiparous process is preceded by the formation of the so-called budding zones (Knospungszone). These arise in *Ctenodrilus*, according to Kennel ('82, pp. 403, 404), between two dissepiments in the middle of a metamere, and new ones are continually formed behind the others as the animal grows in length by cell proliferation at the tail end. The budding zones are, according to Kennel, regions composed of embryonic cells. I think it probable that this embryonic tissue has been derived from the embryonic tissue of the anal end of the animal. There are as many budding zones produced as there are new metameres added by the anal growth, and since the budding zones are intrasegmental, each zoöid consists of four parts; viz. (naming them from anterior to posterior end) of the posterior half of the preceding budding zone, of the posterior half of the metamere in which the budding zone arose, of the anterior part of the next following metamere, and, finally, of the anterior part of the following budding zone. Zoöids then are made up of parts of two adjacent metameres, and the middle of each zoöid is intersegmental. The zoöid has progressed little beyond the state of possessing two (half) metameres at the time it becomes free. New metamères must become formed by caudal growth. The animal is, then, according to my conception of the significance of the process, derived chiefly from these budding zones. Evidently, the law of production of new individuals (or new budding zones) is a simple one, and may be written, in accordance with my nomenclature,

(19) * E (*) * D (*) * C (*) * B (*) * A

in which A, B, C, etc. represent successive individuals (adjacent halves of two metameres), and the asterisks, as before, embryonic tissue. The two adjacent asterisks together represent the budding zone, of which the posterior half (parenthesized) proves itself the least active.

The conditions given by Semper ('77, pp. 69, 77) for *Chætogaster* (and Nais) are much more complicated, but may be expressed by the use of a formula constructed upon the same plan. Chætogaster differs from Ctenodrilus in this: that young budding zones, and eventually young individuals, are produced between older ones, instead of always at the anal end; and the new zoöids often acquire several metameres before becoming free. It seems to me probable that, as in Ctenodrilus, the budding zones are derived ultimately from the anal zone; but here, in contradistinction to Ctenodrilus, new budding zones may secondarily arise from other budding zones produced earlier, thus giving rise to the phenomena of young individuals interpolated between older ones. Representing, then, individuals by the budding zones from which they have arisen, we may convert the following formula of Semper into one based on our own nomenclature:

$$az. - \overbrace{3+0}^{E} - 0 \quad \overbrace{4+0}^{D} - \overbrace{1+0}^{H} - 0 \quad \overbrace{4+1}^{B} - \overbrace{1+0}^{G} - 0 \quad \overbrace{4+0}^{C} - \overbrace{2+0}^{F} - 0 \quad \overbrace{4+1}^{A}$$

in which the succession of generations of zoöids is

. . . 5, 4, 8, 2, 7, 3, 6, 1.

In the above formula A, B, C, etc. represent zoöids; the numerals below the letters, the number of metameres of which each is composed; 0, an incomplete metamere about to be derived from a budding zone; *az.*, the anal zone. Written in accordance with my conception of the facts, this formula would read:

(20) ✱ D (*) * C (*) * a (*) * B (*) * b (*) * a (*) * a′ (*) * A,

which somewhat resembles Formula (15) of Halistemma, and signifies that two embryonic masses are left behind by the anal zone, of which the one anterior to the zoöids proper (represented by letters) goes merely to form the head parts, and is represented parenthesized. The second is caudad the zoöid, and may form a secondary "anal zone" giving rise to new zoöids. From one zoöid two or more anal zones may take their origin. Thus, from the embryonic mass caudad of A there have arisen that caudad of b, which has given rise to b (*) * a (*), and that caudad of a′, which has given rise to a′ (*).[1]

The most general formula given on page 81 undergoes many modifications in the different groups, but in the midst of these modifications certain laws are to be discerned, to some of which I have already called attention. I will now proceed to a discussion of the significance of these laws.

The *quincunx* arrangement of individuals, which is so noticeable in the phytoid stocks of Bugula, and in creeping corms like Lepralia or Cristatella, may be explained as affording additional strength on the one hand, and as a device for saving space on the other.

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[1] From a study of surface views of many specimens of Autolytus collected at Newport during June, 1891, I am convinced that the sexual individuals are produced by proliferation of cells in the metamere XIII. or XIV. of "parent form," — the last which remains behind after breaking off of sexual form. Representing the proliferating metamere by (✱), we may write the budding formula of Autolytus thus:

(20^{a}) ✱ E (*) D (*) C (*) B (*) A (*)

in which the parenthesized asterisks indicate the proliferating, but not gemmiferating anal metameres of the sexual form. (Cf. A. Agassiz, '63, pp. 397–400.)

The absence of true dichotomy, which I have sought to show characterizes the budding of Bryozoa, is interesting as seeming to indicate the fundamental similarity of the process of budding in Paludicella to that found elsewhere. The tip of the branch does not divide equally in the first nor in the other instances, but constantly maintains its precedence, giving off parts of itself to form lateral branches. These parts may grow out at right angles to the primary branch, as in Paludicella, but generally they grow forward nearly parallel to it, as in most marine Gymnolæmata.

In Bugula (Plate VII. Fig. 64ᵃ) branches are always given off *toward the axils*, and therefore an ancestral branch gives off all lateral branches from one side and the successive orders of branches are given off alternately to the right and left. In Crisia, on the contrary, branches are given off *abaxially*, and they are given off not from one side only, but alternately to the right and left. In both cases the two facts are mutually dependent. The first case gives rise to a stock in which the branching tends as greatly as possible towards compactness and the formation of a closely built stock; the second case gives rise to a diffuse and loosely built stock (cf. Figs. 64, 65, and 64ᵃ, 65ᵃ). In the second case there is a maximum space to each individual; in the first, a maximum *economy* of space.

The rule that lateral buds on two closely related branches tend to arise in the same generation is one that, as has been shown, is more or less apparent in some cases, but is easily obscured by other rules. May not the tendency be due to the same causes that produce the synchronism of division in related cells of a cleaving egg?

That lateral buds should occur in *Bugula flabellata* on the outermost rows only is not surprising when we reflect that there is abundant room on the margin, whereas the inner individuals are hemmed in from lateral expansion by the pressure of adjacent rows. This is very marked in certain repent colonies, as, for instance, occasionally in Membranipora (Plate VIII. Fig. 70). Here the intermediate branches 6, 7, 8, and 9 have produced no lateral buds for many generations, while almost every individual of the marginal rows has given rise to a lateral branch. It is merely a result of the same cause, it seems to me, that lateral budding occurs more frequently in *Bugula turrita* at the margins of fans than elsewhere. Here there is room to spread.

The rule (5) that ancestral rows contain fewer *generations* of individuals than lateral ones may perhaps receive a partial explanation from the further fact (rule 6) that of the two rows starting from any axil the ancestral branch will give rise to a greater *total number* of individuals than the lateral one will in the same time. We should expect a less rapid forward growth if the lateral growth is extremely vigorous. One might also say that the intermediate rows had grown abnormally in length, since that is the direction in which there is most room.

The reason why the ancestral branches in Bugula give rise to the greater total number of individuals is, to my mind, because they are marginal. In Crisia it is the lateral branches which are the most prolific, and for the same reason.

The existence of the 7th rule in mat-like species is a mechanical necessity; in the phytoid species, like Bugula and Crisia, it must be accounted for on another ground; namely, on the relations of food supply to demand, — on the deterrent effects of overcrowding. And this, to my mind, is the key to the significance of the 4th, 5th, 6th, and 7th rules. The form of the stock is determined by the same law which has determined the form of the individuals, — the struggle for existence and the survival of the fittest, — the fittest in the present case being those which are most advantageously placed with reference to food supply. Abundant food supply has made possible the rapid production of lateral individuals at the margin, and less abundant food supply has retarded such production in the middle. Therefore has lateral budding occurred more rapidly at the margin; therefore has the number of individuals produced at the margin been greatest; therefore have the median rows grown *in length only* with great rapidity; therefore has the distance between adjacent rows of individuals in phytoid stocks remained constant.

Many observations on different groups of animals agree in demonstrating a relation between rapidity of the budding or fission process and food supply. Thus Zoja ('90, pp. 25–27) has shown for Hydra, and Zacharias ('86, p. 274) and von Wagner ('90, p. 360) for Turbellarians, that abundant food supply results in an acceleration of the processes of non-sexual reproduction, and Braem ('90, p. 24) has shown that budding in Cristatella proceeds less actively during the late fall. This diminution in activity has been attributed by Braem to diminished temperature; but we know also that this period is one of scarcity of the small fresh water organisms upon which the fresh water Bryozoa live (cf. Parker, '90, pp. 597–600), and this fact also must be considered as having an important influence in this case.

II. Relation of the Observations on Budding in Bryozoa to the Germ Layer Theory.

No question in Bryozoan morphology has been more thoroughly discussed than that of the part played by the germ layers in the production of the polypide, and upon none has there been less agreement. Nitsche first boldly opened the question, and concluded that we have in this process a fatal objection to the idea of the homology of the germ layers, in so far as their homology depends upon a similarity of fate throughout the Metazoa. A single layer, the invaginated ectoderm, gives rise to the outer covering of the tentacles, to the pharynx, and to the brain, — structures elsewhere considered as ectodermal, — and also to the lining of the alimentary tract, elsewhere universally accounted entodermal. In view of these facts, "sind die Keimblätter," concludes Nitsche ('75, p. 398), "keineswegs mit einer besonderen histologischen Prädisposition ausgestattete Zellschichten, sondern lediglich die flächenhaft ausgebreiteten Elemente, aus denen die den Metazoenkörper zusammensetzenden, ineinander geschachtelten Röhren sich bilden." Prouho, although recognizing the facts to be as stated by Nitsche, has not discussed the theoretical bearing of the question. Seeliger ('89^a, p. 204) finds in the budding process of Endoprocta a shortening and confusion of the embryonic process. "Wie die gesammte Knospenentwicklung verkürzt ist, erscheinen auch die beiden Processe der Einstülpung durch welche im Embryo zuerst Entodermkanal, dann Atrium sich bilden, in einen zusammengezogen." In another place (Seeliger, '90, p. 595) the budding process is considered as an "immer sich erneuerende Gastrulationsvorgang." Braem ('90, p. 116) regards the inner layer of the bud as entoderm, and the process of its formation as one of gastrulation. In a preliminary notice published last February (Davenport, '91, p. 279) I suggested that the embryonic tissue from which the inner layer of the polypide arises is to be regarded as "neither ectoderm nor entoderm, but as still indifferent, and capable of giving rise to either." A few weeks ago I saw for the first time the paper of Oka ('90), in which he offers (p. 145) *a priori* a similar suggestion concerning the significance of the embryonic tissue from which the inner layer of the polypides arises. I am pleased to find that our ideas, thus independently arrived at, are so fully in agreement. My idea of the relation of the germ layers to the layers of the polypide bud chiefly grew out of my studies on the embryology of Phylactolæmata as described in earlier pages.

As there are two layers to the bud, the question of the part taken by the germ layers in the polypide bud may be subdivided into two: What is the significance of the outer layer of the bud? and, What is the significance of the inner?

The *outer layer of the bud* is derived from the cœlomic epithelium. The views of those who have studied the formation of this inner layer of the cystid in Phylactolæmata may be classed in two categories: (1) those in which it is regarded as entoderm, and the process of its formation as gastrulation; and (2) those in which it is regarded as mesoderm. To the former class belong the views of Reinhard ('80, p. 203), Korotneff ('89, p. 403), and Jullien ('90, p. 19); to the latter, those of Kraepelin ('86, p. 601) and Braem ('90, p. 116), and in this class the views of Barrois ('86, p. 68) and Haddon ('83, p. 543), founded on *a priori* considerations, must be placed.

It seems to me that, since, as Barrois has demonstrated, there is a great similarity between the Phylactolæmatous and Gymnolæmatous larvæ, and especially since the former show evident signs of degeneration, we are bound to study the phenomena they exhibit in the light of our knowledge of the ontogeny of Gymnolæmata.

But first it is necessary to give reasons for believing that the larva of Phylactolæmata is to be regarded as homologous with that of Gymnolæmata; and to do this I will first name the points of similarity in the two larvæ, and then try to show that the differences which exist are not sufficient to invalidate the attempt to establish a homology. And, first of all, it may be said that, since the adult Phylactolæmata and Gymnolæmata are strikingly similar to each other, and since no one doubts their close relationship, we should expect *a priori* that their larvæ would be homologous, especially since the larvæ of Gymnolæmata are admitted to belong to the trochosphere type, of whose ancient origin there can be little doubt. In the second place, the very existence of a larval stage in Phylactolæmata is indicative of its inheritance from an earlier condition, for two reasons: (*a*) because in general fresh-water life tends to eliminate larval stages from species which have inherited them from marine ancestors, and tends little to form them *de novo* (Hydra, fresh-water Turbellarians, Rotifera, Oligochæta, Hirudinea, Astacus, and fresh-water Mollusca); and (*b*) because, specifically, the early stages of development of Phylactolæmata are passed within a uterus-like sac, from which the embryo is released only when a colony is already well established. In the third place, the Phylactolæmatous larva possesses, in common with all Gymnolæmatous larvæ, the following characteristics. The primary polypides arise in both at a pole, and this pole is in both a prominent disk, surrounded by a circular fold, — the so-called mantle fold, — from which it is separated by a circular groove, — the so-called mantle cavity. This organ has a similar origin and fate in the two groups, as shown by Barrois.

The following points of difference, however, must be recognized. First, the absence of a definite ciliated ring, *couronne* (Barrois), of an internal sac, and of a pyriform organ. But, as Barrois ('86, p. 67) has shown, these are absent, or at least (Ostroumoff, '87, pp. 182, 183) little developed, in Cyclostomatous Bryozoa. The ciliated ring and pyriform organ are doubtless organs connected with a free locomotive larval life, which is greatly abbreviated in Phylactolæmata. A second difference exists in the fact that, while most Gymnolæmatous larvæ possess either, rarely, (1) a functional alimentary tract, or (2) a mass of loose tissue lying inside of the ectoderm, the Phylactolæmata possess (3) a central space lined by an epithelium placed next to the ectoderm. However great the difference between the first and third conditions mentioned above, it is to a large extent bridged over by the widespread existence of the second. In some Cyclostomes, moreover, a similar condition to that in Phylactolæmata seems to exist. Compare Metschnikoff ('82, p. 310, Taf. XX. Fig. 62). Lastly, the origin of two primary polypides, instead of one, at the aboral pole, upon which Barrois has laid some stress, cannot be considered a very strong objection to the homology, because in reality the two polypides do not arise at the same time even in Plumatella, and in Cristatella this difference is still more pronounced. In fact, it is not the formation of *two polypides* which requires explanation, but that of a young *stock* before hatching.

There remains, therefore, to my mind, no serious objection to regarding the larvæ of Phylactolæmata and Gymnolæmata as having been derived from some common ancestral larva, possessing, of course, more points of resemblance to the Gymnolæmatous than to the Phylactolæmatous type; and therefore it is perfectly justifiable to interpret the latter by aid of the former.

Admitting the larvæ to be homologous, we should expect the process of *gastrulation* to be comparable throughout Ectoprocta. As a matter of fact, we do find a great similarity in the earliest stages. Thus, the first indication of the inner layer is the ingression of four cells at one pole, which by multiplication give rise to a layer of cells lying inside of the ectoderm.[1] It is to the comparative study of the fate of this inner layer in the different Ectoproct larvæ that we must look for an explanation of the layer in the specific case of the Phylactolæmata.

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[1] This has been shown for Membranipora (Tendra) by Repiachoff ('78, pp. 416–420); for Alcyonidium polyoum by Harmer ('87, pp. 445, 446); for Bugula by Vigelius ('86, p. 519); and for Cristatella in the present paper (page 68).

For the purposes of this study, it is desirable to begin with species in which there has been a minimum amount of degeneration. Such are Membranipora (Cyphonautes), Alcyonidium, and Flustrella, to which we must now turn our attention.

The studies of Repiachoff on Membranipora lead up to a stage in which the entoderm lies as a solid mass inside the ectoderm, and is separated from it at all points. Neither the origin of the mesoderm nor the formation of stomodæum or proctodæum was observed at this time. As for the fully formed Cyphonautes, it is certain, as I can confirm from personal observation, that there is a well developed functional alimentary tract, and that it is provided with a well developed muscular system, including cross-striped muscle fibres. There is, therefore, every reason for believing that typical entoderm and mesoderm have been formed in it.

In Alcyonidium (polyoum), Harmer ('87, p. 445) has shown that after gastrulation a great mass of cells occupies the former blastocœl. This, in the author's opinion, represents entoderm and mesoderm. The young larva possesses a mouth, an œsophagus, and a large stomach, but never an anus. No evidence is presented that the oral pole corresponds with the pole of ingression.

Flustrella, which is nearly related to the last species, possesses in its young larval stages a pocket, which Prouho ('90, pp. 424–426) has shown to represent the anterior part of the alimentary tract, directly comparable with that of Alcyonidium polyoum, but less developed. Muscle fibres and an epithelial lining of the entoderm and ectoderm exist to indicate the presence of mesodermal tissue.

These three genera, Membranipora, Alcyonidium, and Flustrella, are the only Ectoprocta in whose larvæ the presence of an alimentary tract has as yet been demonstrated.

In Bugula, a very careful study of which was made by Vigelius ('86 and '88), one finds after gastrulation and cell multiplication a mass of cells filling the whole interior of the larval body, at first appearing as an epithelium surrounding a central space, but later without arrangement and often showing signs of degenerescence. No definite separate mesoderm could be found, and at no time was any trace of an alimentary tract to be seen. Vigelius calls the mass derived from the four entodermal cells *Füllgewebe*, and he believes it to correspond morphologically to both "hypoblast and mesoblast." It is to be noted, however, as a point of considerable importance, that in his figures of the metamorphosing larva Vigelius ('88, Taf. XIX. Fig. 6) represents this tissue as having almost entirely disappeared; that which remains giving rise to the mesodermal lining — the outer layer of the bud — of the developing polypide.

There can be no doubt that the so-called oral pole of the Bugula larva corresponds to the mouth-bearing pole of Alcyonidium, but does it correspond to the pole of ingression of entoderm? This question has not been answered by Vigelius. The existence of homopolar stages like that represented in his ('86) Figure 25, Taf. XXVI., makes it very difficult to establish this doubtful point.

The formation of the inner layer of Cyclostomes has been studied by Barrois ('82, p. 141). He says: "Dès les premiers stades les sphères vitellines glissent les unes sur les autres de manière à former une espèce de gastrula par épibolie et l'on ne tarde pas à rencontrer des stades d'un volume extrêmement exigu et déjà composés d'une couche exodermique et d'une masse endodermique libre dans son intérieur. La masse endodermique s'atrophie rapidement et l'on arrive à une petite blastula qui succède non pas à un stade composé de cellules radiaires dans lequel se forme une cavité centrale, mais qui est issu, au contraire, d'une vraie gastrula née par épibolie dans les premiers stades de la segmentation et dans laquelle la masse endodermique est déjà disparue." I have quoted Barrois thus at length, since his description will show forcibly at least one thing, that the fate of the cells which by ingression had entered the blastocœl is quite different from that of those in Bugula, where a great *Füllgewebe* is formed. Ostroumoff ('87, p. 183), however, has shown that the inner layer of the Cyclostome larva does not disappear, but comes to line the ectoderm as a very thin layer. In the adult larva, however, we find the contents of the ectodermal sac "filled with mesenchymatous cells, which are commingled with yolk granules and globules of albumen." It is these cells that produce the very considerable mesodermal layer of the first polypide, which arises in the metamorphosis of the larva. Here, as elsewhere, an apparently homopolar stage intervenes between gastrulation and the formation of larval organs, making orientation difficult.

Thus, passing from Cyphonautes, through Alcyonidium and Flustrella, Bugula, and finally Cyclostomes, we have a series in all of which the inner germ layer is derived from one pole by ingression or by 'epiboly," and in which there is a gradual reduction of the functional entoderm until it seems, in Cyclostomes, to be lost, and a gradual transformation of the mesoderm from a cell mass nearly filling the larva, and producing muscles and a lining to the body wall and alimentary tract, to a single thin cell layer lying next to the ectoderm, or to mesenchymatous cells extending through the cœlom.

This same series may be said, also, to be one in which there is a gradual decline in the complexity of larval organs. These find their maximum development in the bivalve Cyphonautes and Flustrella, and the complicated and beautiful Alcyonidium larva. They find their minimum development in the Cyclostomes, whose larvæ, instead of a girdle of flagella, possess merely an undifferentiated clothing of cilia, are reduced to a cylindrical or ellipsoidal form, lack the pyriform organ of other species, and in some cases possess only the rudiment of the internal sac.

If we were to imagine still another term at the degraded end of the series, it would be a form in which the four inner-layer cells that arise by ingression at one pole of the larva should give rise to little or absolutely no entoderm, in which the mesoderm should come to form an inner lining to the ectoderm, and in which the internal sac should be entirely absent. It is just these conditions which are fulfilled by the Phylactolæmatous larva.

Of all these changes, the loss of the entoderm is the most striking. What can be said in explanation of it? I would suggest this hypothesis: that *the entoderm of the Bryozoan larva has become rudimentary through loss of the alimentary function.*

In direct support of this hypothesis I have little experimental evidence to offer. One observation, however, which I made last summer, seems to favor this conclusion strongly. This is that larval life is of considerable duration in Cyphonautes, which possesses a functional alimentary tract, but is very brief in Bugula, in which no alimentary tract arises. As is well known, Cyphonautes occurs in enormous numbers in the "tow" at certain seasons of the year, and this is alone evidence of a considerable length of life. I have taken Cyphonautes thus obtained from the tow and have kept them for three or four days, at the end of which time they died, or had settled to the bottom of the glass vessel to undergo their metamorphosis. In fact, from several hundred Cyphonautes which I collected, not more than half a dozen completed their full metamorphosis, the others apparently succumbing to unfavorable conditions.[1]

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[1] Just as the manuscript of this paper is going to the printer, after long delay caused by an accident necessitating the re-engraving of the plates, I find that Dr. Prouho read last summer ('90), before the Association Française pour l'Avancement de la Science, a preliminary communication on the development of Cyphonautes. This is published in the printed report of the proceedings of that association. The

The *Bugula* larvæ, on the contrary, I have never found in the tow, but they swarm out from stocks gathered in the morning and placed in a glass vessel; and I can confirm Nitsche's ('69, p. 9) observation that they settle and begin their metamorphosis within "a few hours" after hatching. One rarely or never finds these larvæ succumbing to the unfavorable conditions of the aquarium before metamorphosing. From these observations I conclude that the Bugula larva has a very much shorter life than Cyphonautes. Now, since the larva, owing to its shortened life, has no need of functional entoderm, and since entoderm can be of use to the larva only, no part of it going over into the tissues of the primary polypide of the stock (except as food material), functional entoderm is not developed. In other genera, its rudiments have become less and less important in the ontogeny, and, finally, in Phylactolæmata are wholly lost.

That the entoderm should reach its last stage of degeneration in *Phylactolæmata* is easily understood when we consider that the larval period is passed in a closed oœcium, from the wall or neck of which it receives nourishment *as a parasite does.* Moreover, by the delay in the period of hatching, as well as by precocious development of polypides, one at least of the latter is usually functional in the just hatched stock, for there is sometimes found at least one polypide in the newly hatched larva, which is partly extruded, and therefore capable of feeding, and thus of supplying the whole stock with nutriment. Of what advantage to a species could be the development of a functional larval entoderm, which should go to form no part of its adult tissue, provided the larva was contained in a uterus during its early stages, and was provided with the adult digestive organs in a functional condition before leaving the uterus?

Those who maintain that the inner layer is to be regarded as entoderm, and are still unwilling to place the Bryozoa among the Cœlenterata, must account for the absence of mesoderm. Korotneff ('89, p. 400) finds degenerating cells in the blastocœl before this is wholly obliterated by the extension of the inner layer. These he seems to regard as degenerate mesoderm. According to his view, then, the entoderm gives rise to the muscularis, — for this arises from the inner larval layer, according

author does not there state whether stomodæum and proctodæum are formed on the blastoporic side of the larva. He accounts for the existence of an alimentary tract in Cyphonautes by the fact that it undergoes its development disconnected with the parent, while almost all other Bryozoa pass their early stages in the parent or some protecting zoöid (oœcium, ovisac, ovicell).

to Braem's ('90, Taf. VII. Fig. 89 *mb.*) observations, which I can abundantly confirm, — and to the cœlomic epithelium of the adult stock. In the few series of sections of the proper stage which I possess, I have not found with certainty the degenerating cells of which Korotneff speaks; but even if they regularly occur, I should be inclined to regard them as the degenerated entoderm, the mesoderm persisting to give rise to the muscular tissue and the cœlomic epithelium.

From a consideration of these facts, — that the larvæ are homologous and the process of gastrulation is comparable throughout the Ectoprocta, that in the least modified larvæ both functional entoderm and mesoderm are produced by that gastrulation, that one of these two germ layers has become rudimentary in Phylactolæmata, that it is highly probable that the entoderm has disappeared from loss of function, and that the layer which persists gives rise to the musculature, sexual cells, and cœlomic epithelium, — I conclude that *the inner layer of the Phylactolæmatous larva, and therefore the outer layer of the bud, is mesoderm.*

If we accept the point of view of Kleinenberg ('86, pp. 1–19) and admit the existence in general of only two layers, ectoderm and entoderm, a clearer conception of the modification undergone by the Phylactolæmatous larva may be gained. We may divide the entoderm arising in Bryozoa into two parts; viz. (1) that which gives rise to the lining of the midgut, as in Cyphonautes, and (2) all the rest of the inner layer. Now, since no midgut is formed in the Phylactolæmatous larva, part (1) of the entoderm has ceased to be differentiated; all which remains, then, is part (2); but this is equivalent to "mesoderm" in the sense in which I have employed it, and therefore I am justified in saying that "mesoderm" only is produced.

The question has now to be answered, What is the significance of the *inner layer of the bud?* Two different answers have been given to this question. It has been maintained, on the one hand, that it is to be regarded as ectoderm; on the other, as entoderm. There are serious difficulties in the way of accepting the first view, — so serious, in fact, that few authors have maintained it, although at first glance it seems to be required by the facts. Although we have not yet sufficient grounds for declaring that organs formed by budding must be built up from the same germ layers as corresponding larval ones, — although we may admit that gemmigenesis recapitulates phylogeny and corresponds with ontogeny only in an imperfect and confused way, — still, from the experience gained by tracing the development of hundreds of animals from the most widely separated groups of the animal kingdom, the idea that a functional alimentary tract is ever wholly derived from differentiated ectoderm will not be accepted by most embryologists without conclusive evidence.

The second view is that the formation of the inner layer of the bud is a process of gastrulation, giving rise to entoderm, and that the so-called "gastrulation" of the sexual ontogeny of Phylactolæmata is to be regarded as a precocious ingression of mesoderm only.

Two considerations are opposed to this view. In Membranipora there is a gastrulation which gives rise to the entoderm and mesoderm of the larva; and since the gastrulation of Phylactolæmata is similar, these elements must be potentially present here also. The "gastrulation" in Bryozoa is a normal one; if there is any entoderm in the body wall giving rise to the inner layer of the bud, it must have been entoderm which failed to become invaginated. But what, in the second place, is to be gained by assuming that the inner layer of the bud is formed from entoderm? Here is as great a difficulty as before, since the nervous system originates from this layer. It has been maintained in many cases that the nervous system arises from *mesoderm,* and Seeliger ('89, p. 602) believes that it is formed from that layer in the non-sexual reproduction of some Tunicates; but I know of no good evidence of its origin in any of the Triploblastica from *entoderm.*

Before going on to state my conception of the significance of the inner polypide layer, I desire to call attention to the conditions in the region at which it is first formed. I have shown above (page 69) that the primary polypide or polypides arise from the pole of ingression in Phylactolæmata, and that therefore in this group the aboral pole (in the sense of Barrois) corresponds to the pole of ingression. As I understand Barrois, he means by oral pole merely the pole which in Cyphonautes, for instance, bears the mouth, — the pole also by which the larva attaches itself. Braem ('90, p. 123, foot-note), however, interprets "oral side" in Barrois's sense to mean in the last instance the place at which gastrulation takes place. Perhaps Barrois does somewhere state such to be the significance of his term (I have not found the place), but in that case I can only say that, to my mind, he has not produced sufficient evidence to prove that the oral pole of the larva of Gymnolæmata is the same as the pole of ingression in the gastrula; nor, in my opinion, has any other investigator done so. Nearly all species studied have a stage early in their development when their poles are very similar, and orientation certainly would be exceedingly difficult. One of the best figured series in which to trace the homology of poles is that shown by Repiachoff ('80, Taf III.) for Bowerbankia. So far as the figures go, one would conclude that Figure 10 A and its predecessors were oriented in the opposite direction to Figure 11 and its successors, which would result in placing the pole of ingression (Fig. 9) at the aboral pole of the larva, — the pole which here, as in all other Gymnolæmata, and, I believe, in Phylactolæmata also, gives rise to the primary polypide. I have given above additional evidence for this conclusion, in my argument to prove the homology of the larvæ and larval organs in Phylactolæmata and Gymnolæmata.

The polypides arise in Phylactolœmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolœmata. The pole of ingression, or the region of the lips of the blastopore, must be regarded as being a region of less pronounced differentiation than the rest of the gastrula. Its cells cannot be said to be either ectodermal or entodermal. It is an interesting fact, that it is just these indifferent cells — not yet either ectoderm or entoderm — that give rise to the inner layer of the polypide, from which organs usually considered ectodermal as well as those considered entodermal arise.

My conclusion, then, the objections to which I fully realize, may be stated in the following words: *The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore. Such cells are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.*

Just when and where, on this hypothesis, the differentiation into ectoderm and entoderm occurs, is an important question; but unfortunately I cannot answer it decisively. It may be pointed out, however, that it has now been shown for most Ectoprocta that the lining of the middle part of the alimentary tract is formed independently of the œsophagus, and by an actual or potential outpocketing of the primitive simple sac of the bud. In Endoprocta there is a similar outpocketing, which, however, arises in connection with the œsophagus, and is formed independently of the rectum.

This is perhaps the proper place to call attention to the fact that the mesodermal outer layer of the bud has a very embryonic character at the budding region. This is indicated by the fact, that in Phylactolæmata (in which group alone I have studied the subject) eggs always arise from that part of the cœlomic epithelium which lies in the budding region (cf. Plate XI. Fig. 93). In Pyrosoma, also, according to the researches of Seeliger ('89, pp. 598–602) the mesoderm of the budding region, the stolon, gives rise to eggs. The same condition seems to exist in other Tunicates.

III. On some Characteristics of Gemmiparous Tissue.

In the preceding part of this paper the words "embryonic tissue," "undifferentiated tissue," have often recurred, and they are terms in wide usage in modern zoölogy. I do not know of any attempt to define further the real character of this tissue, nor to give its more detailed characteristics, other than that usually employed in the term *plasmareich*, or "rich in plasma." The persistence of yolk granules is, as Nussbaum ('80, pp. 2–14) and Goette ('75, pp. 31, 32, 831) have shown in the case of amphibian embryos, indicative of the *embryonic* condition of cells, when these have been derived from an egg filled with yolk.

It is very far from my purpose to go into a detailed discussion of the significance of embryonic tissue, for which I am not yet fitted; nevertheless, I wish to call attention to the minuter characters of gemmiparous tissue as I have found it in Phylactolæmata and Paludicella. I have described it in some detail in preceding pages.

First, then, gemmiparous tissue seems to stain more deeply than non-gemmiparous tissue in the same section. This character has been repeatedly observed before by others, and Braem calls attention to it several times. I have already described how I found, by the use of high powers, that much of this depth of stain was due to the unusually large number of deeply staining granules scattered through the cell, but chiefly gathered about the nucleus (Figs. 6, 17, 18, etc.). So marked is the greater depth of the stain around the nuclei, that, with a power so low that the nuclei are hardly distinguishable, their position is indicated by a deeply staining band.

Secondly, gemmiparous tissue, as I have found it in the cases referred to, is distinguished by the possession of large cells, nuclei, and nucleoli. I had already noticed this fact in my studies on budding in Cristatella, and I find that Braem has figured the nuclei in the budding region as larger than the average (cf. Braem, '90, Taf. VII. Figs. 86, 88–90). My own figures show this repeatedly (Plate I. Figs. 3, 4, 5, 6, Plate II. Figs. 15, 17, Plate XI. Fig. 99, etc.). I have also noticed this to a certain extent in the marine Bryozoa, but, since the cells of the latter are smaller, and as I did not succeed in obtaining from them sections so satisfactorily stained, the results are not so reliable. In attempting to obtain an explanation of this phenomenon one involuntarily recalls to mind the condition in young egg cells, where the nucleus attains a relatively enormous size. This great size of the nucleus in young egg cells is explained by Korschelt ('89, p. 92) as due to its participation in the trophic activity of the cell: "Sein grösster Umfang fällt in die Zeit des energischen Wachsthums der Eizelle." So in the gemmiparous regions the large size of the nuclei must be considered as connected with the growth of the cells.

But if the growth of the cells is accompanied by a rapid ingestion of food material (which the larger nucleus implies), some evidence of that fact should be observed in the cells themselves in the presence of food granules. Such food material in rapidly growing ovarian egg cells lies near the nucleus. Stuhlmann ('87, pp. 13, 14) describes such a condition in the ovary of Zoarces. "Neben dem Keimbläschen, jedoch ein klein wenig von seiner Membran entfernt, bilden sich an verschiedenen Stellen jetzt eigentümliche Verdichtungen des Protoplasmas, die sich ein wenig stärker mit Saffranin färben als das Zellplasma." Such a thickening of the protoplasma is represented in the figures as minute granules. Korschelt ('89, pp. 123–125) mentions several other such instances.

It has seemed to me possible to interpret the stainable granules lying near to the nucleus in gemmiparous tissue as such food material,[1] particularly since we know that food material does exist in the cœlomic epithelium lying next to the cells which are about to divide rapidly and to give rise to the inner layer of the polypide. That food is being taken in by the inner layer cells from the cœlomic epithelium is indicated by the fact that the nuclei of the former cells lie near the latter epithelium (cf. Figs. 15, 17, 18, 28, 56, etc.); for, as Korschelt has shown, the nucleus tends to move towards the centre of activity of the cell. That these granules observed in the cells are food material is indicated by their abundance in cells lying next to the reticulated cells of the cœlomic epithelium (Figs. 6, 28, 56).

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[1] Granules similar to these appear to exist in the protoplasm of all cells. It is their extraordinary abundance in the gemmiparous tissue upon which I lay stress. They have been variously interpreted by different authors. Bütschli ('88, pp. 1469–1472) describes various kinds of stainable granules in Ciliata which are food products, and the general character of which accords with that of the granules referred to above. "Excretion granules" of Ciliata do not stain, according to this author, which is an indication that the bodies in gemmiparous tissue are not such. I am particularly struck by the fact that the food products of Protozoa are chiefly found in parasitic forms, — Gregarinidæ and parasitic Ciliata. These take up food in solution from their hosts exactly as the cells of the body wall of Bryozoa do from the body cavity. Altmann ('90) has recently interpreted similar deeply staining granules in other cells, as "die Elementarorganismen." I can see no reason, on Altmann's theory, for the peculiar distribution of the granules that I have found.

My conclusion, then, is this: *Gemmiparous tissue is a rapidly assimilating tissue, possessing large nuclei because actively assimilating, and staining deeply because full of food material.*[1]

While for Nussbaum, as already quoted (page 71), "indifferent cells" are essential to the reproduction of individuals by non-sexual as well as by sexual methods, Seeliger ('90, p. 596) has concluded that "die Vorgänge bei der Knospung der Bryozoen uns zeigen, wie histologisch sehr bestimmt differenzirte Gewebe einen ganz embryonalen Charakter wiedergewinnen können. Mehr noch als bei der normalen Knospung am freien Stockende ist dieses Vermögen bei der Regeneration der Polypide der Ektoprokten oder der Köpfchen der Pedicellinen ausgebildet. In diesen Fällen sehen wir ein plasmaarmes, äusserest feines Plattenepithel, das über sich eine mächtige Cuticula ausgeschieden hat, sich in kubische und cylindrische plasmareiche Zellen zurückverwandeln und durch eine Einstülpung ein neues Polypid bilden, in welchem schliesslich die mannigfachsten Gewebsformen vertreten sind."

It seems to me that many facts in the budding of Bryozoa are strongly in favor of Nussbaum's hypothesis. On this assumption, we can best understand why in Cristatella there is not an invagination of the ectoderm, and why instead a stolon is formed in the embryo, which passes along at the base of the ectoderm and at intervals gives rise to the inner layer of the body wall. I believe it is because the outer layer of the body becomes so rapidly differentiated by the secretion of the gelatinous balls in its cells as to be incapacitated for the work of building organs. In Plumatella the outer layer of the body wall, which is derived, as Braem has shown, from the neck of the older polypide, retains for a long time its embryonic condition, so that its deeper cells can and do go to form the inner layer of the polypide bud.

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[1] Other observers describe gemmiparous tissue as being either rich in food or deeply staining. Seeliger ('85, p. 588) speaks thus of the mesodermal gemmiparous tissue in Salpa: "Die einzelnen Zellen sind grossblasig, enthalten einen runden Kern und führen Oel- und Fettsubstanzen die als Reservematerial beim Aufbau des embryonalen Leibes weiterhin in Verwendung gelangen." Von Wagner ('90, p. 877) says of the indifferent cells which are being transformed into the new pharynx of dividing Microstoma: "Dieselben nehmen an Grösse zu, . . . indem gleichzeitig ihre Protoplasmaleiber feinkörnig granulirt und für Farbstoffe imbibitionsfähiger werden."

In some sections of gemmules of Esperella fibrexilis, H. V. Wilson, of which Dr. Wilson has very kindly sent me several slides, I find the outer layer of young gemmules, in which the inner layer has been newly formed, stained very deeply. Observed with a Zeiss Apochr. 4.0 mm., Ocs. 8 and 12, the cell contents are seen to be evidently of two kinds, — light and deeply stained. The latter appearance is due, in part at least, to small dark granules, which can be discerned without much difficulty.

On Nussbaum's hypothesis we can best understand why in Paludicella the *Anlagen* of the lateral branches exist from the beginning as cuboidal cells, quite different from those of the rest of the body wall; we can understand why the cell layers of the margins of the stock, the tips of branches, and the ends of stolons from which buds arise, are thicker and more rapidly dividing than the rest of the body wall (cf. Figs. 14, 71, 73, 75); and we can also understand why the regenerating buds always arise from the region of the neck of the degenerated polypide, — the same region from which that degenerate polypide had arisen by budding.

There is no doubt, however, that at times buds do arise from tissue which, as Seeliger says, has lost its cuboidal nature only to regain it. From such tissue apparently the polypide of Figure 79 has arisen; from such tissue certainly, as Seeliger says, do regenerating polypides arise. But is the process by which cuboidal cells become a pavement epithelium one of so fundamental differentiation that, in accordance with Nussbaum's doctrine, we should not expect, under favorable conditions, to see these cells regain their cuboidal form? No doubt we have many other cases in the animal kingdom in which flat epithelial cells regain their cuboidal form. Thus, for instance, among the Bryozoa, Oka ('90, p. 132) has shown how the flat cells of the outer layer of the statoblast begin to thicken again at the return of warmth, and at the beginning of the active assimilative processes, not only at the pole from which the primary polypide is to arise, but also opposite to this.

Many facts indicate that cells may become flattened epithelia, and yet not lose their embryonic character. Maas ('90, pp. 541–544) has recently shown step by step how the columnar ectoderm of the fresh water sponge is forced, on account of the great increase in surface which it is called upon quickly to cover, to become broad and flat. It finally gives rise to an epithelium so flat that its existence was long overlooked, and has been denied by so competent an observer as Goette; and yet in its flattened condition it possesses to a remarkable degree the capacity of sending out pseudopodia-like processes, a condition indicative much less of a high degree of differentiation or specialization, than of an unspecialized, primitive or embryonic condition.

I have already stated (page 65) that the region from which the regenerating buds of Cheilostomes arise, although one of flattened epithelium, is one in which many more nuclei persist than elsewhere in the adult (cf. again Fig. 71). This fact, coupled with the constancy of position of regenerating buds with reference to the degenerated polypide, is to my mind evidence against the assertion that buds arise here from "*histologically very definitely differentiated tissue.*"

As for regeneration in Endoprocta, no one is more competent to speak than Seeliger himself. I am the more surprised, therefore, to find that in Ascopodaria macropus, which is quite closely allied to the species studied by Seeliger ('89), the cells at the part of the stalk immediately below the "head," from which regenerated buds arise, are, as Ehlers's magnificent Pedicellina work shows, very large and cuboidal (Ehlers, '90, Taf. II. Figs. 26–33). I think one may conclude that a similar condition obtains in some cases in Pedicellina, even judging from Seeliger's own drawings, although they are drawn to a scale that is not quite large enough to allow of settling this point (Seeliger, '89, Taf. X. Fig. 35, *a*, Fig. 41, etc.).

If the increase in size of the flattened cells, and their subsequent rapid division and invagination to form a bud, are due to their more active nourishment, it would be difficult to see why certain cells of any region should quickly undergo this modification, while the adjacent cells apparently as favorably situated with reference to the acquirement of food retain their flattened, quiescent condition, if we assumed such favorable situation to be the only requisite. Still less satisfactorily would such an assumption explain the regular position of regenerating buds. It is taking only one step farther back, but, to my mind, a helpful step, to assert that cell proliferation in any region which produces invagination depends upon the capacity of the cells of that region to become better nourished than their fellows. This may evidently be effected by a diminution in the feeding capacity of the surrounding cells, or by an increase in this respect in the growing cells.

IV. Relationships of Endoprocta and Ectoprocta.

I discussed this topic in my earlier paper (Davenport, '90, pp. 132, 133). I have only to add, that later studies have confirmed my opinion of Nitsche's correctness in placing these two groups close together, and in regarding the Endoprocta as nearer the ancestral types. The stages of Figures 25 (Plate III.) and 77 (Plate IX.) probably represent roughly a phylogenetic stage ancestral to both groups of Bryozoa, but most clearly allied to adult Endoprocta. The formation of new tentacles anteriorly and posteriorly in Figure 77, would reproduce the adult Endoproct condition. Two changes lead to the Ectoproct stage: first, the closure of the tentacular corona posteriorly *in front* of the anus (Plate V. Fig. 43), and, secondly, the formation of the pharynx or anterior part of the œsophagus by the growth of the oral tentacles over the floor of the atrium towards the atrial opening. Thus the brain, which lies at the floor of the atrium in Ectoprocta, comes to lie on the pharynx. The pharynx would, upon this assumption, be a new structure, not found in Endoprocta. Such appearances as are exhibited by Figure 77 lead me to retract my former expressed opinion, in which I agreed with Nitsche in saying that the earliest condition of the tentacular corona is a U-shaped one. Rather, the tentacles are formed first on each side of the atrium, and only secondarily grow around the mouth in front, as later they grow in between mouth and anus. The U-shaped stage is therefore not the primary one, but secondary.

The close relationship of Endoprocta and Ectoprocta has recently been doubted by Cori ('90, p. 16), but his chief argument depends upon the dissimilarity of the Endoproct and Ectoproct kidney. Unfortunately, our knowledge of the latter is still very imperfect, and we may well hope for renewed researches in the subject by this skilful investigator.

Ehlers ('90, pp. 149–154) has recently re-expressed his former ('76, p. 132) utterances concerning the lack of homology between the tentacles of Ectoprocta and the "cirri" of Endoprocta. He finds the homologue of the latter in the "Diaphragma" or "Kragen" of Ectoprocta. This is the organ which I have believed to be homologous with Kraepelin's "Randwulst" (which may be Anglicized as marginal thickening), — an organ occurring in all Ectoprocta. It is nothing but the "neck of the polypide," which has sunk below the general level of the body wall. It is always provided with sphincter muscles, and in Ctenostomes forms the base of insertion of the cylindrical or comb-like "collare setosum." It can hardly be that Ehlers refers to this latter structure by the term "Kragen," since this is merely cuticular. In my opinion the "Diaphragma" of Nitsche cannot be homologized with the cirri of Endoprocta, because it is merely a part of the body wall comparable to that part from which the "polypide" of Endoproctous Bryozoa arises, and *beneath* which the tentacles or "cirri" arise. This part of the body wall is provided with a sphincter in Endoprocta as well as Ectoprocta, and by it the atrial cavity may in both cases be closed.

To my mind, the most significant difference between the two groups exists in the fact that the outpocketing to form the stomach arises from the oral end of the future alimentary tract in Endoprocta, and from the anal end in Ectoprocta. One is led to believe that in the ancestral form either two nearly equally important outpocketings from both the oral and anal sides existed, or that the two existing methods are remnants of a method different from either (such as the formation of the whole alimentary tract at once), or, finally, that the Endoproct condition represents the ancestral one, and that the rectal evagination has secondarily become of greater importance in Ectoprocta, and that the oral evagination has become less significant. Oka ('90, pp. 134, 141) has recently asserted that in the polypide buds of the statoblast and adult colony of a Pectinatella of Japan (P. gelatinosa) the œsophagus and stomach are formed by one evagination, which acquires secondary connection with the rectum. This condition reminds one, then, of Endoprocta. I must, however, doubt the accuracy of Oka's conclusions until more satisfactory evidence is forthcoming; the more so, since Pectinatella magnifica, Leidy, presents a method of budding exactly comparable to that in Cristatella and Plumatella, as my own sections show with sufficient clearness.

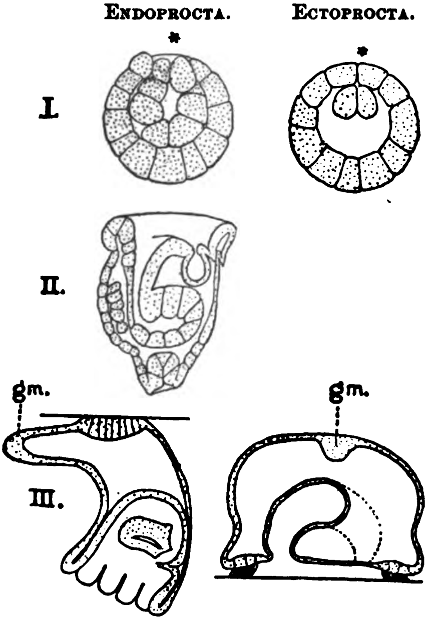
The homology of the Ectoprocta and Endoprocta implies a homology of their larvæ, and demands that the life history of the two groups should be directly comparable.

It is well known from the researches of Hatschek ('77) on Pedicellina, and of Harmer ('85) on Loxosoma, that the surface of the larva which bears the mouth and anus, i. e. its oral side, corresponds with that of the blastopore. How, then, is the oral aspect of the Ectoproct larvæ, which I have tried to show is opposite to the pole of the blastopore, to be homologized with this?

The mouth and anus of the Endoproct larva undergo a rotation after the larva has settled, so that they come to occupy the pole opposite to that at which the blastopore was. This stage of the Endoproct larva is comparable to the whole larval stage of Ectoprocta. I believe the two stages to be homologous, and that, just as polypides are *precociously* formed upon the Phylactolæmatous larva, its larval digestive tract having dropped out from the ontogeny, so the mouth and anus of Gymnolæmata are *precociously* formed on the pole opposite the blastopore, the primitive stage during which they existed at the blastoporic pole having dropped out of the ontogeny.

It is well known from the works of Harmer ('86) and Seeliger ('89), that in Pedicellina, in which the metamorphosis of the larva has been best studied, the stolon arises from the base of the stalk — that is, at the pole where mouth and anus were first formed — at the pole of invagination. I have shown that this is true for Phylactolæmata, and probably for Gymnolæmata.

If the interpretation which I have put on Gymnolæmatous ontogeny becomes confirmed, the larvæ and the budding areas will be homologous throughout all Bryozoa. The following diagrams will explain my idea of the relation of the different ontogenetic stages in the two groups.



The left hand vertical series represents stages in the development of Endoprocta; the right hand one, stages of Ectoprocta. The blastopore (*) is throughout turned upwards in the figures. Stage I. is in both cases a young gastrula. Stage II. is that of the free-swimming larva of Endoprocta. This stage is lost in the ontogeny of Ectoprocta, in which, by abbreviation of larval life, the free-swimming stage corresponds to the condition of the fixed Endoproct after it has undergone its rotation. This stage, or one slightly later, is shown in III. Both larvæ are fixed, the Endoproct by the blastoporic, the Ectoproct by the opposite pole. The position of the stolon, or of the first polypide of the colony produced by non-sexual methods, is represented at *gm.*, near the blastoporic pole.

Summary.

The following general scheme of the budding process in Ectoprocta, derived from my own and other recent studies, may be now drawn up. The references are to pages of this paper.

All Ectoprocta build stocks or corms. The individuals in these are arranged in rows radiating from a centre, — the larva or statoblast, — and are placed one in front of another (Figs. 2, 64^a, 65^a, 67, 71^a, etc.).

New rows or branches are constantly being produced peripherally. There is no dichotomy in the branching (page 86), but the ancestral or median branch gives rise to one or more lateral branches, which in turn become median branches of their part of the stock.

The body wall and polypides of the median branch, as well as the *Anlagen* of lateral branches, arise from a pre-existing mass of embryonic tissue, the gemmiparous mass (pages 72–82). This may exist centrally of the forming region, as in Phylactolæmata, or peripherally, as in Gymnolæmata.

The anal aspect of the polypide is turned towards the gemmiparous mass (page 82).

The outer layer of the body wall in the budding region is one of rapidly assimilating and rapidly dividing tissue; the inner layer of the body wall becomes filled with food taken from the body cavity in species in which the latter is early cut off by a partition (Paludicella, Bowerbankia, Lepralia ?); it shows no tendency to do so in species with a cœnocœl (Phylactolæmata, Alcyonidium).

The first impulse to the formation of the polypide is found in the outer layer of the body wall (excepting when this is highly modified, as in Cristatella), and many cells seem to be involved in its formation from the beginning (pages 8, 56).

This outer layer of the body wall is embryonic tissue, derived from the tip of the stock (margin of the corm) as in Gymnolæmata, or from the neck of pre-existing polypides, as in Phylactolæmata. It is the direct descendant of the gemmiparous tissue of the larva, which in turn has been derived from the region around the blastopore, — in Phylactolæmata certainly, in Gymnolæmata probably (pages 8, 11, 12, 69).

The inner layer of the body wall is also embryonic in the budding region, as indicated by the fact that ova arise near the neck of the polypide, in Phylactolæmata at least (page 68).

The outer mural layer becomes the inner bud layer by invagination, with or without the formation of a cavity. In the former case (many

Gymnolæmata) the mouth of the invagination pocket rapidly closes to give rise to the neck of the polypide (page 56). In the latter case, the cavity of the bud arises only secondarily by a separation of its walls (page 18).

By a rapid growth of the walls of the bud, its distal part, in which the alimentary tract is to arise, is formed. Since this rapid growth occurs earlier at the anal side than at the oral, the rectum is formed first, the stomach last (pages 19, 57).

By an approximation of the lateral walls, alimentary tract and atrio-pharyngeal cavity become separated.

The œsophagus arises as a pocket of the atrio-pharyngeal cavity, and secondarily unites with the stomach (pages 19, 58).

The lophophore arises first as two lateral thickenings of the atrio-pharyngeal wall, then as two lateral folds, whose cavity becomes the ring canal (pages 20, 58),

Tentacles appear on the ridge of the lophophoric fold thus established, and like it are formed first at the sides of the polypide, then anteriorly and posteriorly (pages 22, 59).

The posterior end of the lophophoric ridge is the last to be formed, and, in forming, it cuts off the anal part of the atrium from the intertentacular cavity (pages 23, 62).

The compressed intertentacular cavity becomes circular by change in position of the oral tentacles (pages 24, 62).

The ganglion arises as a depression in the floor of the intertentacular room, and becomes included in the pharynx, which is differentiated by the change in position of the oral tentacles (pages 26, 61).

Muscles and funiculi arise from the cœlomic epithelium of both the body wall and the bud (pages 27–31, 63).

The neck of the polypide may sink to a considerable distance below the general level of the body forming the "Randwulst" of Phylactolæmata or "Diaphragma" of Gymnolæmata (pages 31, 63, 103).

The atrial opening first arises at a late period by separation of the cells of the neck.

The communication plate arises in Paludicella as a circular fold of the layers of the body wall, the mesodermal cells at the centre of which become cuticularized. It is not so completely closed as to prevent communication between the cœlomata of the two individuals it separates.

The mesodermal cells of Paludicella become stored with food material before the formation of the communication plate, and yield it up to the rapidly growing bud.

The regenerated polypides, like the marginal ones, arise in Cheilostomes in a definite position, — on the wall of the operculum from tissue left behind to give rise to the polypide, but not wholly used up in its formation. They arise wholly from the body wall, come to lie next to the "brown body," and cause its disintegration.

The more important theoretical conclusions to which I have arrived are: —

a. There is in every stock or corm of Bryozoa a mass of indifferent cell material, which is derived directly from the indifferent cells of the larva or embryo, and whose function is to form the organs of the different individuals, including the polypides. This mass by constant growth and division affords the embryonic material for lateral branches.

b. The form of the stock and interrelation of individuals is in large part controlled by food supply.

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c. The inner layer of the Phylactolæmatous larva represents mesoderm only: the entoderm has become rudimentary through loss of the alimentary function.

d. The polypides arise in Phylactolæmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolæmata.

e. The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore, and they are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.

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f. Gemmiparous tissue is a rapidly assimilating tissue possessing large nuclei because actively assimilating, and staining deeply because full of food material.

g. The Endoproct and Ectoproct larvæ are to be compared by assuming that the act of rotation of the axes occurring in the former has been leaped over in the ontogeny, the mouth and anus arising at once on the pole opposite the blastopore.

CAMBRIDGE, MASS., June 1, 1891.

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PLATE I.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*gn.*	Ganglion.
cta.	Normal cuticula of adult body wall.	*i.*	Inner layer of bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.
ec'drm.	Ectoderm.	*mu. pyr.*	Pyramidal muscles.
ex.	Outer layer of bud.	*œ.*	Œsophagus (pharynx).
ga.	Stomach.	*rt.*	Rectum.
gm.	Bud.	*ta.*	Tentacle.

All figures are of Paludicella Ehrenbergii.

Fig. 1. Stock of Paludicella Ehrenbergii, viewed as an opaque object. × 4.5.

Fig. 2. Diagram representing the interrelations of individuals in stock shown in Figure 1. *A–H* are individuals of the ancestral (median) branch; *a*, *b*, *c*, etc., lateral branches given off from the ancestral branch to the right; *a'*, *b'*, branches given off to the left; *α*, *β*, etc., lateral branches of second order given off in the direction of the distal end of the *ancestral* branch; *α'*, *β'*, etc., given off in the direction of proximal end; $\mathbf{a}_1'$, lateral branches of third order — to left.

Fig. 2^{a}. Diagram of another (smaller) stock. Letters have same significance as in foregoing.

Fig. 3. Cross section of branch near tip, showing the first trace of the bud of the polypide at *ex.*, *i.* × 685.

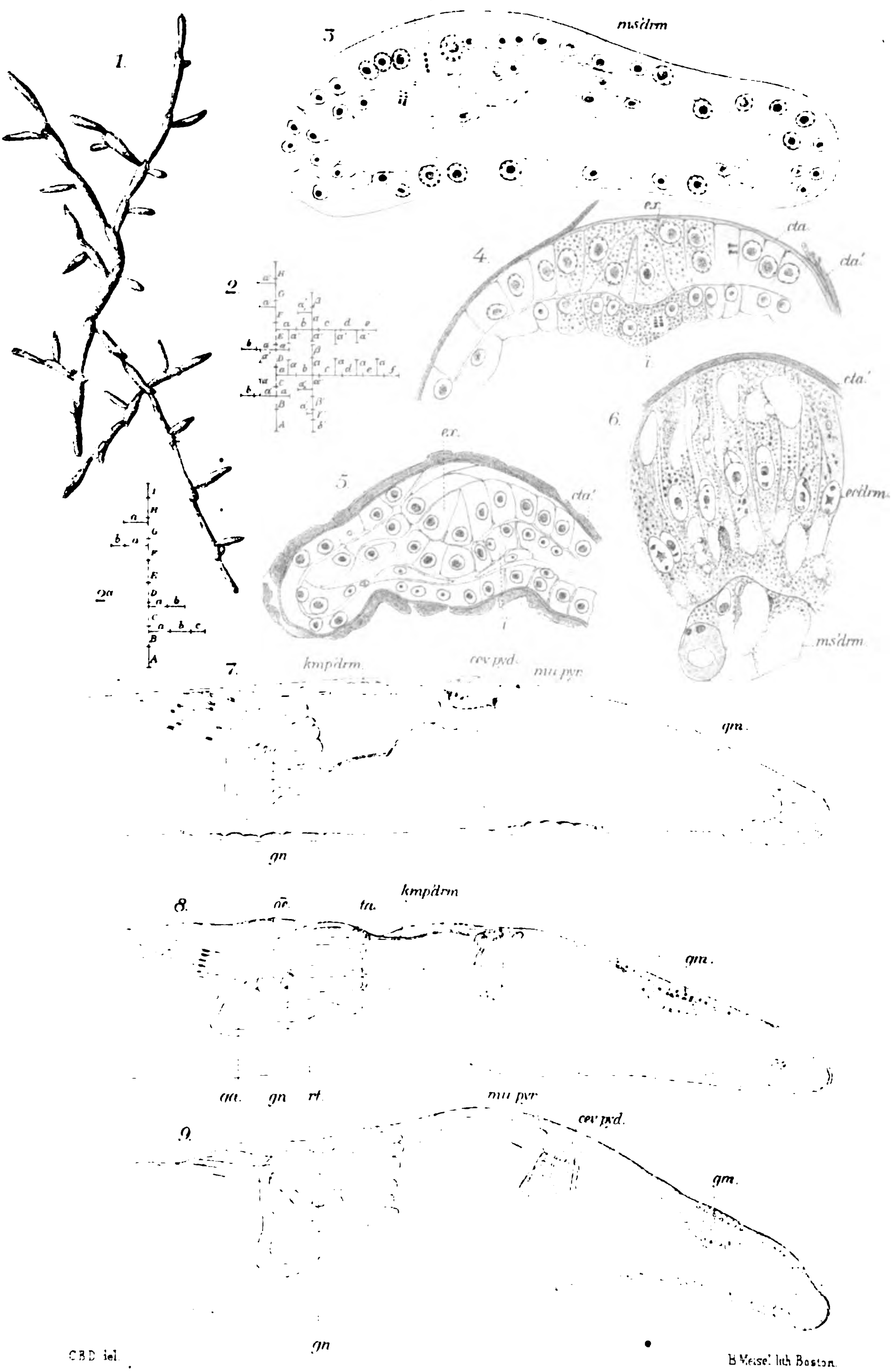
Fig. 4. Cross section of branch near tip, showing bud of polypide slightly older than in Figure 3. × 635.

Fig. 5. Cross section of slightly collapsed branch near tip, showing ingression of cells at *ex.* to form inner layer of bud. × 685.

Fig. 6. Longitudinal section of tip of branch to show cell structure. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1000.

Figs. 7, 8, 9. Optical sections (nearly in sagittal plane) of three tips of branches in successive stages of development, showing relations of young bud, *gm.*, to next older polypide. In Figure 8 the branch is slightly shrunken. × 87.

DAVENPORT. – BUDDING IN BRYOZOA. PL. I.



C B D. del.

B Meisel lith Boston.

PLATE II.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*ec'drm.*	Ectoderm.
cta.	Normal cuticula of body wall.	*gm. l.*	*Anlage* of lateral bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.

All Figures from preparations of Paludicella Ehrenbergii.

Fig. 10. Surface view of cuticula near the end of a branch at intervals, *a* being nearest the tip, and *d* farthest from it. The branch was stained in Erlich's hæmatoxylin, the color being taken up by superficial cuticula only. × 320.

Figs. 11, 12, 13. Cross sections of the cuticula taken at different distances from the tip, to show the stainable and non-stainable cuticulæ. Figure 11 is from near the tip, Figure 13 farthest from it. × 1000.

Fig. 14. Longitudinal median (sagittal) section through the tip of a branch showing cells of tip and an early stage in the development of the polypide. × 410.

Fig. 15. Cross section of branch showing origin of lateral bud. × 635.

Fig. 16. Longitudinal section of body wall of branch through the point at which a lateral bud is originating. Polypide of ancestral branch is nearly adult. × 635.

Fig. 17. Longitudinal section of body wall from near the tip through the *Anlage* of a lateral bud. × 410.

Fig. 18. Cross section of branch showing histological conditions of *Anlage* of lateral bud. The polypide has reached a stage of development corresponding to that of Figure 36, Plate IV. × 1000.

Fig. 19. Longitudinal section through body wall from the same branch as Figure 17, but farther from the tip. Histological conditions are to be compared with those of Figure 17, which represents a less differentiated condition. × 410.

Fig. 20. Cross section of branch in which the polypide has reached a stage slightly younger than that of Figure 36. To show *Anlage* of two lateral buds with their cuboidal undifferentiated cells. × 410.

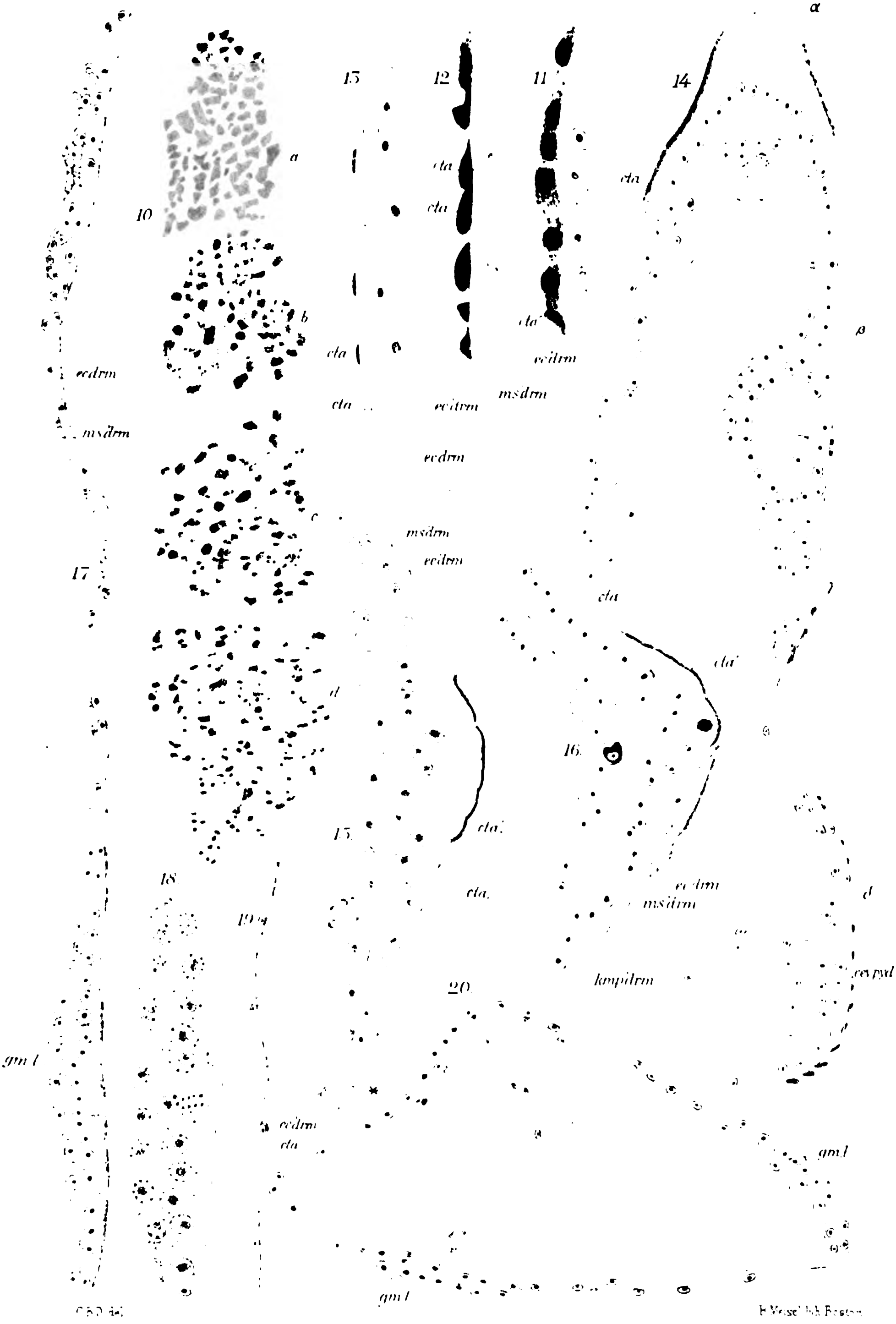


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PLATE III.

ABBREVIATIONS.

An.	Anal side of polypide.	*kmp'drm.*	Kamptoderm.
atr.	Atrium.	*loph.*	Lophophore.
cev. pyd.	Neck of polypide.	*ms'drm.*	Mesoderm.
cl. mu. ret.	Young cells of retractor muscle.	*mu. par.*	Parietal muscle.
		œ.	Œsophagus.
cta.	Cuticula.	*Or.*	Oral side of polypide.
ec'drm.	Ectoderm.	*rt.*	Rectum.
ga.	Stomach.	*vlv. cr.*	Cardiac valve.
gn.	Ganglion.		

All figures from preparations of Paludicella Ehrenbergii.

Figs. 21–25. Longitudinal sections through buds of polypides at successively older stages. The tip of the colony, and therefore the anal aspect of the polypide, is to the right in all cases. All figures × 410.

Fig. 21. Stage of Figure 37 (Plate IV.). Few nuclei in central region.

Fig. 22. Shows rapid growth of bud, chiefly at neck of polypide. The two inner cell layers are about to separate to form the common cavity of atrium and œsophagus.

Fig. 23. Beginning of formation of alimentary tract at rectum, *rt.* The row of nuclei separating the atrio-œsophageal cavity from the alimentary tract is due to the fusion of the two inner layers of the bud along this line.

Fig. 24. Rectum and stomach completed. Retractor muscles begin to form.

Fig. 25. Lophophore and young tentacles have made their appearance, and œsophagus and pharynx are separated from atrium. Beginning of formation of brain at *gn.*

Fig. 26. Part of cross section of a branch of stage of Figure 30. Parietal muscles, *mu. par.*, occupy a diameter of the section, and are attached to the cuticula. × 635.

Fig. 27. Young parietal muscle at stage of Figure 28. This is one of the pair which in a later stage are found lying together in Figure 26. × 635.

Fig. 28. Cross section of branch showing young polypide, and reticulated vacuolated cells. × 410.

Fig. 29. Bit of body wall, with cuticula separated from underlying ectoderm to show ends of parietal muscles. × 630.

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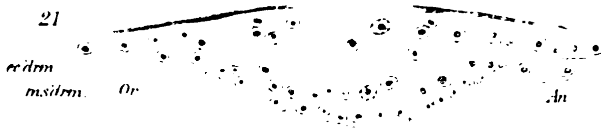

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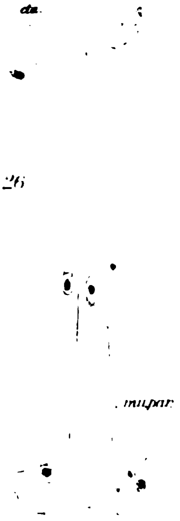

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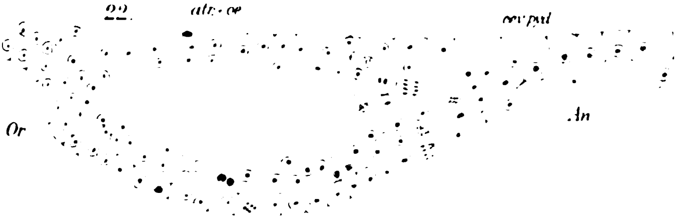

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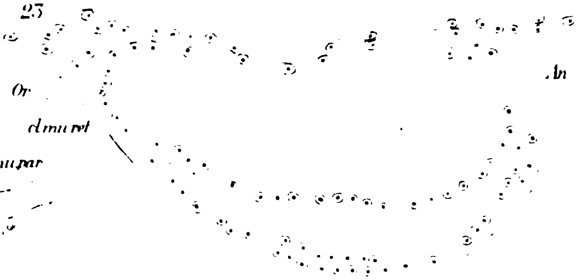

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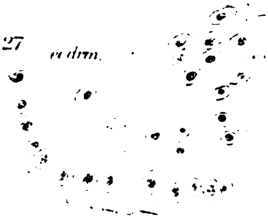

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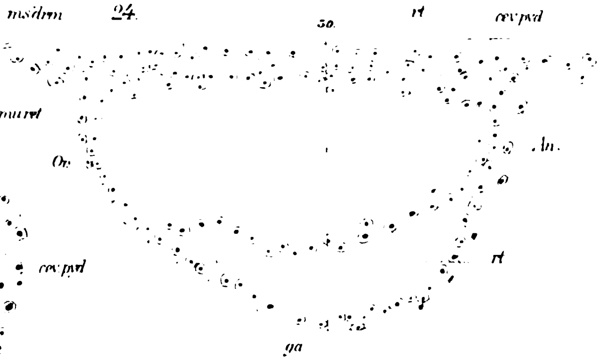

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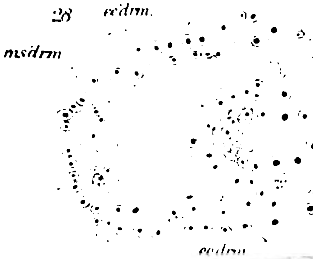

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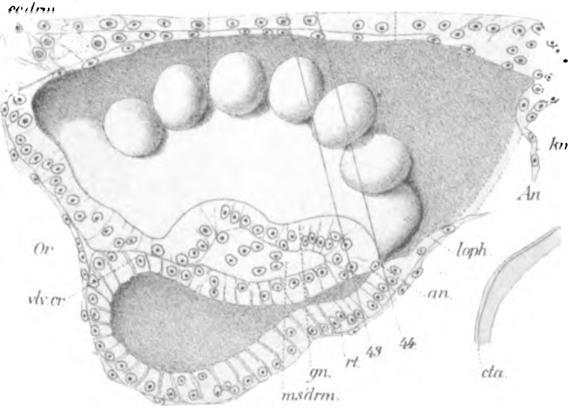

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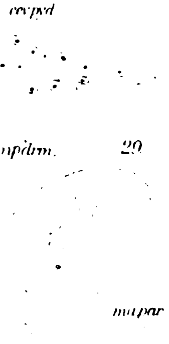

C.B.D. del. B. Meisel lith. Boston.

PLATE IV.

ABBREVIATIONS.

An.	Anal side of polypide.	*i.*	Inner layer of bud.
an.	Anus.	*loph.*	Lophophore.
atr.	Atrium.	*ms'drm.*	Mesoderm.
can. crc.	Ring canal.	*mu.*	Muscle fibre in funiculus.
ec'drm.	Ectoderm.	*n.'*	Circumœsophageal nerve.
ex.	Outer layer of bud.	*œ.*	Œsophagus.
fun. inf.	Inferior funiculus.	*Or.*	Oral side of polypide.
fun. sup.	Superior funiculus.	*rt.*	Rectum.
ga.	Stomach.	*vac.*	Vacuole.
gn.	Ganglion.	*vlv. cr.*	Cardiac valve.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 30. Cross section of polypide bud of stage of Figure 24, Plate III. The position is indicated by the line 30, Figure 24. × 410.

Figs. 31–34. Four cross sections of a branch through a young polypide, somewhat younger than that of Figure 25. Figure 31 is nearer the anal, Figure 34 nearer the oral surface. In Figure 34 that part only of the section of the polypide which lies near the body wall is represented. × 410.

Fig. 35. Cross section of branch through polypide of age of Figure 25. To show origin of tentacles and ring canal. × 410.

Fig. 36. Sagittal section of young polypide at period of closure of ganglion, *gn*. × 410.

Fig. 36^{a}. Bit of same polypide a few sections to one side of plane of Figure 36, showing origin of inferior funiculus. × 410.

Fig. 37. From cross section of branch showing early stage in development of the bud. × 410.

Fig. 38. From a sagittal section of nearly adult polypide, showing the two funiculi and their muscles. × 410.

Figs. 39 and 40. Two neighboring sections parallel to the body wall through a bud of the stage of Figure 23. Figure 40 lies three sections below Figure 39. Figure 39 shows the atrial cavity, formed as yet only on the anal side. Figure 40 shows the beginning of formation of the alimentary tract at the anal end. Note the vacuolated condition of the mesoderm. × 410.

Fig. 41. Polypide of about the stage of Figure 25 looked at *en face*. The anal tentacles, being turned under, do not appear. To show compressed condition of polypide, and alternating position of tentacles. Cf. Figure 77, Plate IX. × 320.

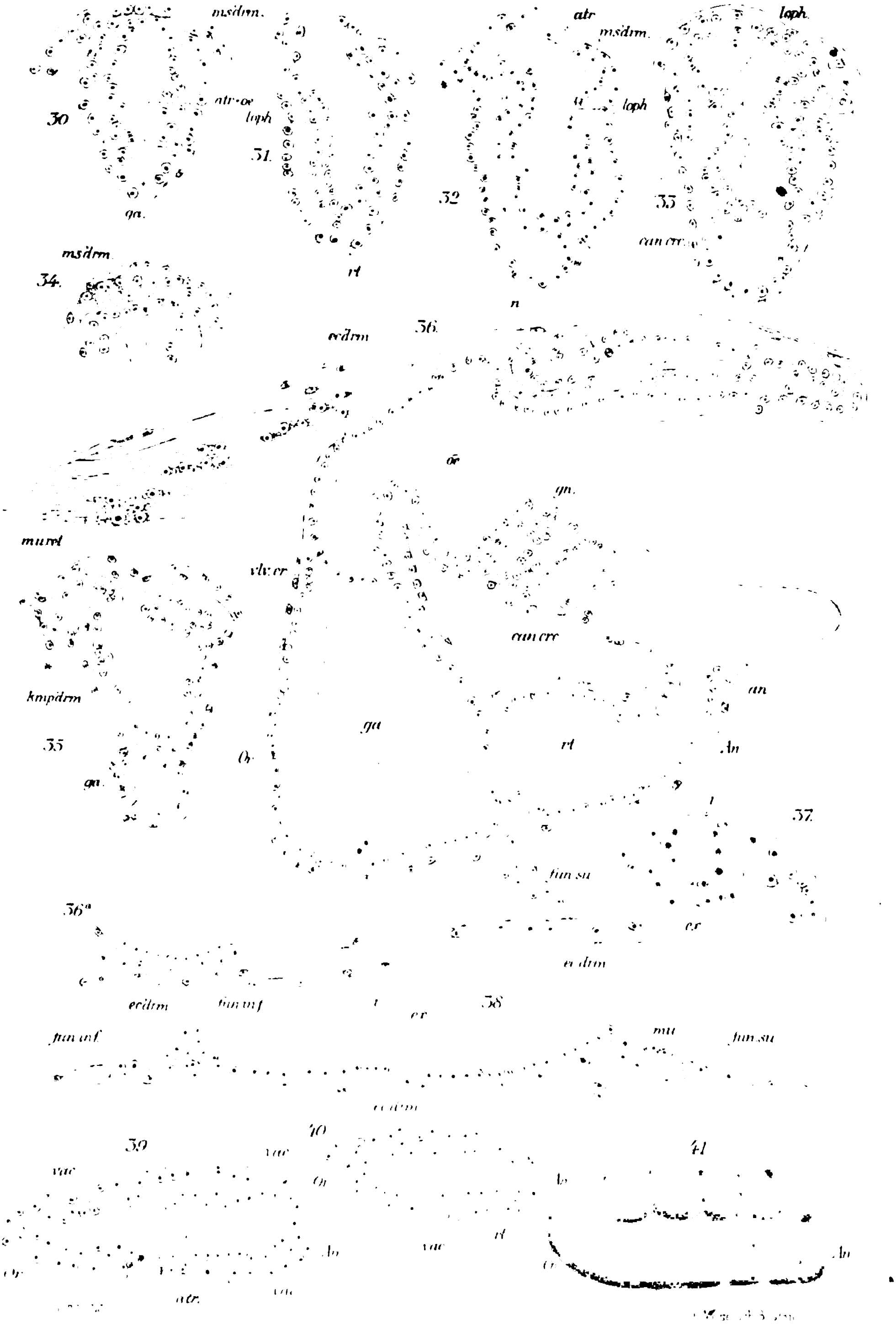
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PLATE V.

ABBREVIATIONS.

an.	Anus.	*kmp'drm.*	Kamptoderm.
cev. pyd.	Neck of the polypide.	*loph.*	Lophophore.
clr. set.	Collare setosum.	*ms'drm.*	Mesoderm.
cta.	Normal cuticula of adult body wall.	*mu. par.*	Parietal muscles.
		mu. pyr.	Pyramidal muscles.
cta.'	Cuticula secreted by the tip of branch.	*of. atr.*	Atrial opening.
		rt.	Rectum.
ec'drm.	Ectoderm.	*spht.*	Sphincter.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 42. Cross section of branch of age of Figure 37, Plate IV., to show origin of primary parietal muscles. × 410.

Figs. 43 and 44. Successive sections through a polypide slightly older than that of Figure 25, cut perpendicularly to the long axis of the branch. During this period the lophophore becomes more nearly circular, and its aboral ends meet oralwards of the rectum, *rt.* Figure 44 is nearer the tip of the branch. × 410.

Fig. 45. Axial section of neck and atrial opening of polypide just sufficiently developed to be capable of extrusion. Shows the collare setosum in place. × 410.

Fig. 46. Section of communication plate cut across the branch. Two sections (10 μ) above Figure 51. × 635.

Figs. 47–49. Three stages in the development of the communication plates. Longitudinal sections of the branch. In Figure 47, the polypide has reached the stage of Figure 22; in Figure 48, the stage of Figure 23; and in Figure 49, the stage of Figure 24. × 635.

Fig. 50. Longitudinal section through neck of young polypide, showing the sinking of the neck below the general surface of the body, and the method of forming the inner cuticula of neck. × 390.

Fig. 51. Cross section of branch through communication plate. The left side of the section includes the cuticula and the underlying flat ectodermal layer. The right side cuts a little lower into the mesodermal cells. × 635.

DAVENPORT – BUDDING IN BRYOZOA.

PL. V.

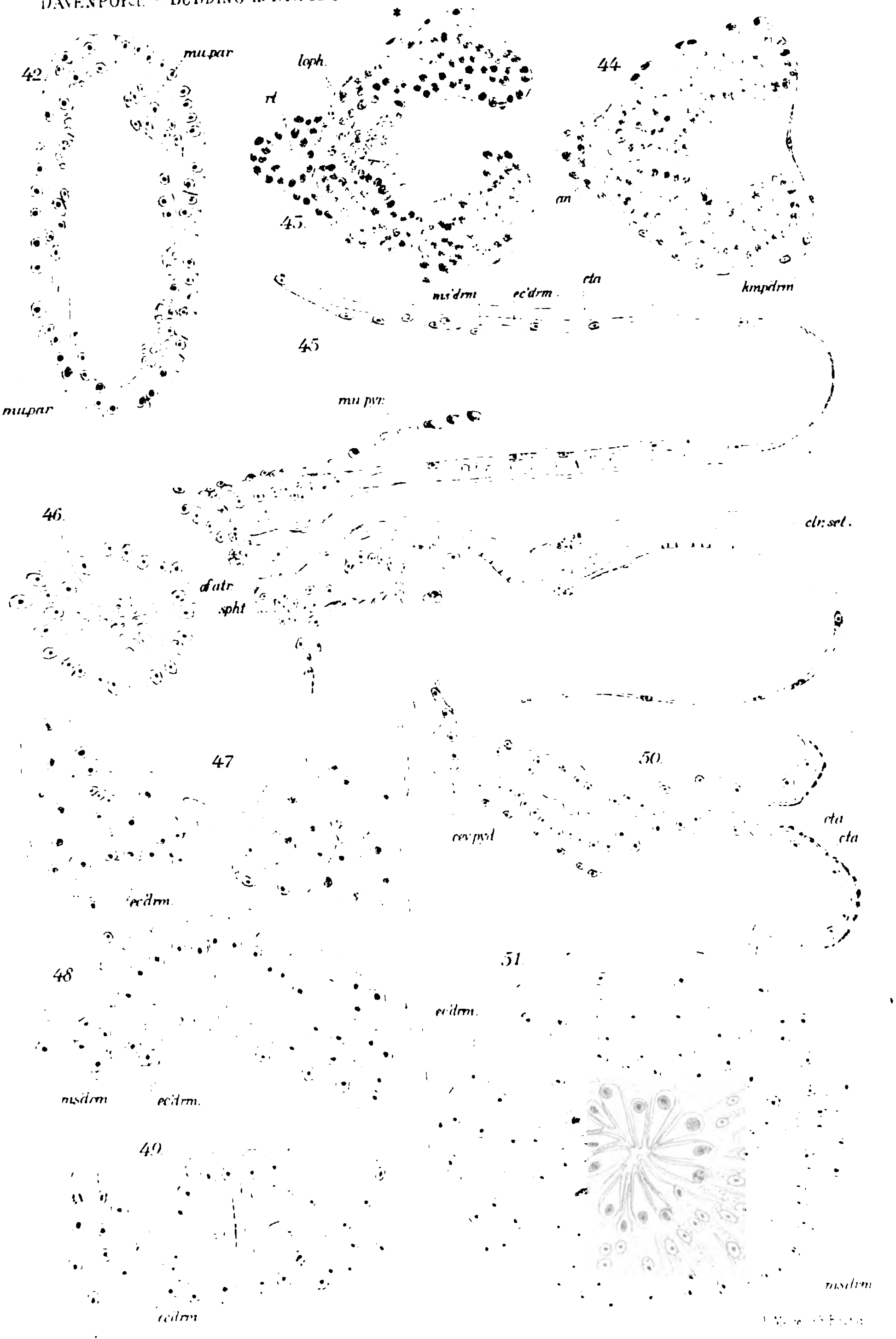


PLATE VI.

ABBREVIATIONS.

an.	Anus.	*i.*	Inner layer of bud.
can. crc.	Ring canal.	*kmp'drm.*	Kamptoderm.
cev. pyd.	Neck of the polypide.	*la. comn.*	Communication plate.
cl. rtl.	Reticulated cells.	*ms'drm.*	Mesoderm.
cta.	Normal cuticula of adult body wall.	*mu. par.*	Parietal muscles.
		mu. pyr.	Pyramidal muscles.
cta.'	Cuticula secreted by tip.	*n.'*	Circumœsophageal nerve.
ec'drm.	Ectoderm.	*œ.*	Œsophagus.
ex.	Outer layer of bud.	*rt.*	Rectum.
gm.	Bud.	*vac.*	Vacuole.
gn.	ganglion.		

All figures from preparations of Paludicella Ehrenbergii.

Fig. 52. Cross section of a branch through a polypide slightly older than that shown in Figure 36. The section passes through the brain and whole extent of the ring canal, together with its opening into the cœlom. × 635.

Fig. 53. Next section below Figure 52 of same series; showing the beginning of the circumœsophageal nerve ring. × 635.

Fig. 54. Shows connection of mesodermal cells of body wall, *ms'drm*, with those of the outer layer of bud, *ex*. × 1030.

Fig. 55. Origin of the secondary parietal muscle cells from mesoderm of body wall. × 635.

Fig. 56. Histological conditions of the budding regions. The cells have large nuclei, the mesodermal cells are vacuolated and rapidly dividing; the cells of the bud are densely granular. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1070.

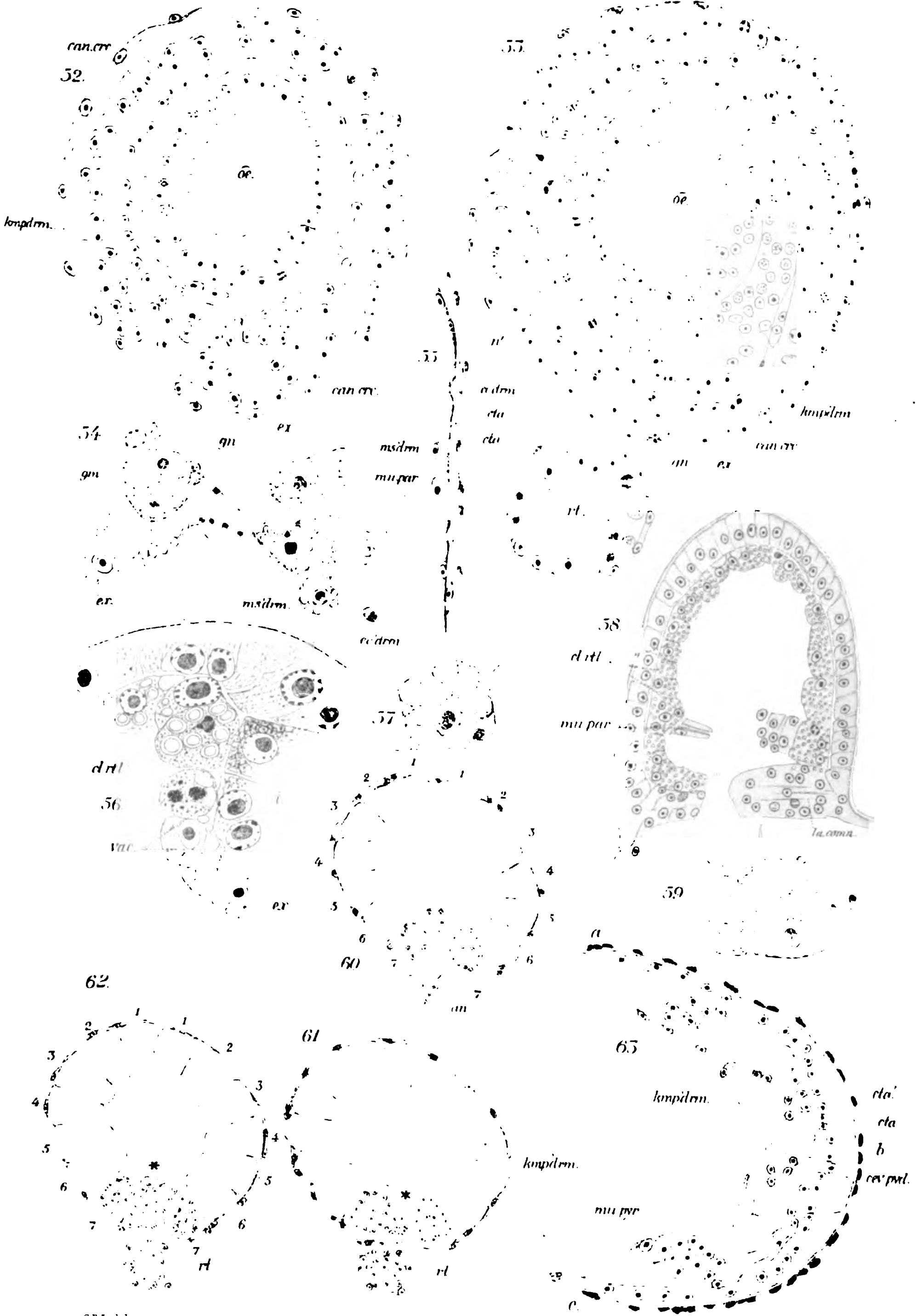
Fig. 57. Normal vacuolated cell, full of food particles. × 1080.

Fig. 58. Longitudinal section of young lateral branch, showing highly reticulated character of mesoderm, and nearly complete formation of communication plate. × 410.

Fig. 59. Reticulated cell, showing one of the pseudopodia-like processes which frequently appear on them, projecting into the cœlom. × 1080.

Figs. 60–62. Three successive sections from a series across the tentacles of a polypide which has 15 tentacles, and is of about the stage of Figure 36. The odd tentacle (*) is shorter than the others, and lies opposite the rectum, *rt*. × 295.

Fig. 63. Cross section of branch through neck of polypide of about the age of Figure 36. Shows also the young pyramidal muscles. × 410.



C.B.D. del.

F. Meisel lith Boston

PLATE VII.

For explanation of notation employed on this plate, see page 41.

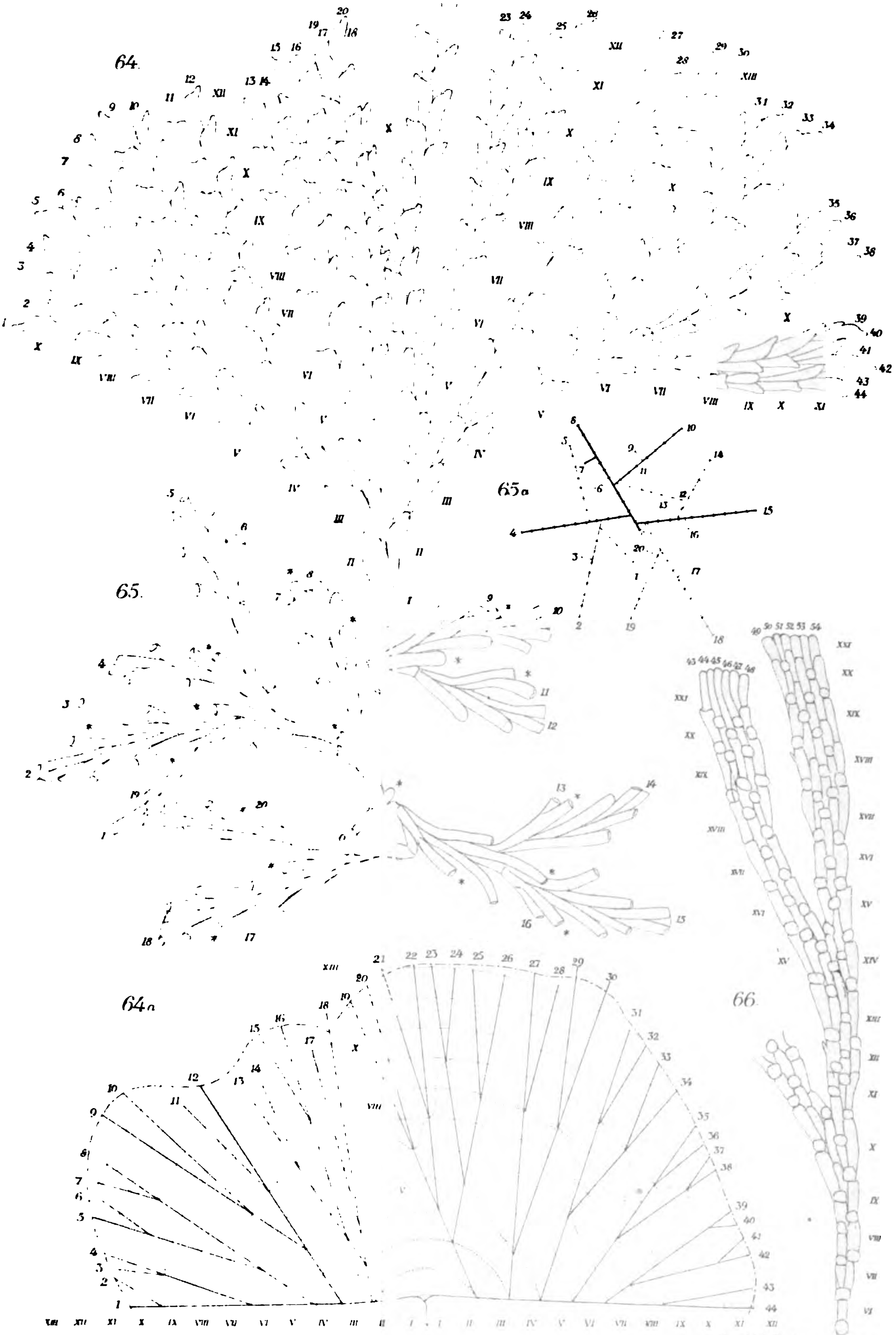
Fig. 64. **Outline drawing of one of the lateral "fans" of *Bugula turrita*, taken from the axis of the colony and spread out flat on the slide. × ca. 12.**

Fig. 64a. **Diagram showing arrangement of individuals in Figure 64.**

Fig. 65. **Outline drawing of one of the lateral branches of a stock of *Crisia eburnea*, spread out flat on the slide. × 16.**

Fig. 65a. **Diagram showing arrangement of individuals in Figure 65.**

Fig. 66. **Part of stock of *Bugula flabellata*. × 10.**



C. B. D. del.

B. Meisel, lith. Boston.

PLATE VIII.

ABBREVIATIONS.

op.	Operculum.
pyd. dgn.	Degenerated polypide.
pyd. rgn.	Regenerated polypide.

Fig. 67. Diagram to show interrelation of individuals in the corm, Figure 69.

Fig. 68. A part of a corm of *Membranipora pilosa*, to show regular arrangement, with a single median branch, each of whose individuals gives rise to two lateral branches. The * indicates margin of frond on which stock was growing. × ca. 8.

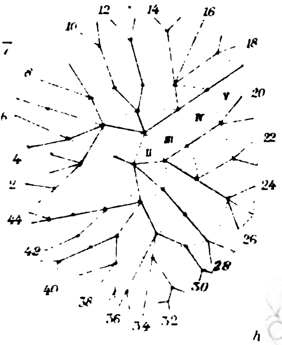
Fig. 69. Young corm of *Flustrella hispida*, to show arrangement of individuals. × 10.

Fig. 70. Young corm of *Membranipora pilosa*, with several median branches, showing regular arrangement. The marginal ones alone give rise to lateral branches. × 10.

Fig. 71. Young corm of *Lepralia Pallasiana*, showing arrangement of individuals. On the left, the nuclei of the cells of the body wall are shown, to indicate the inequality of their distribution. On the right, nuclei are omitted. At *pyd. rgn.* a regenerating polypide is seen, on the operculum. × 43.

Fig. 71ᵃ. Plan of Figure 71.

67



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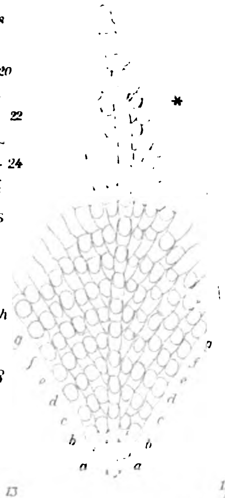

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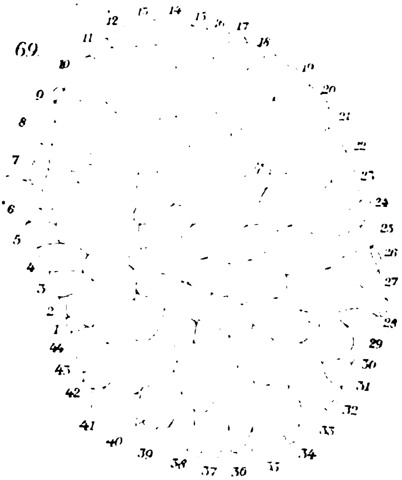

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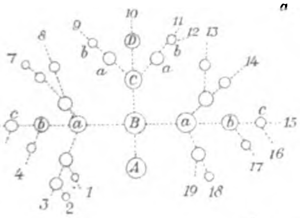

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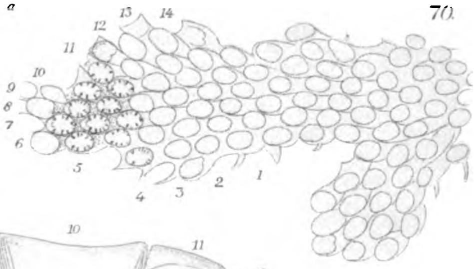

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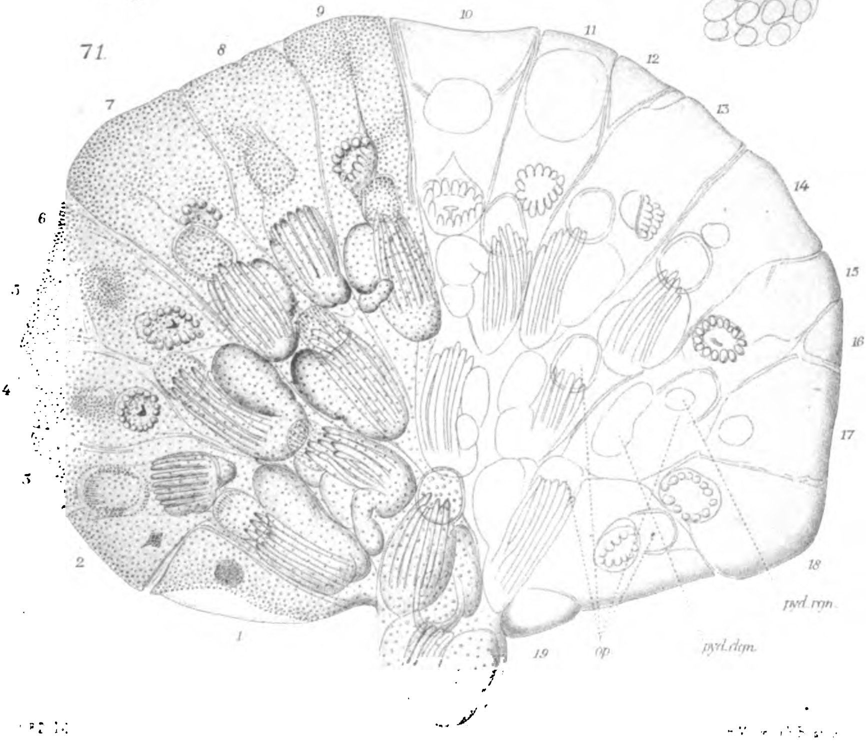


PLATE IX.

ABBREVIATIONS.

An.	Anal side of polypide.	*lu. gm.*	Lumen of bud.
atr.	Atrium.	*marg.*	Margin of corm.
can. crc.	Ring canal.	*ms'drm.*	Mesoderm.
cev. pyd.	Neck of the polypide.	*n.'*	Circumœsophageal nerve.
cta.	Cuticula.	*œ.*	Œsophagus.
ec'drm.	Ectoderm.	*Or.*	Oral side of polypide.
ex.	Outer layer of bud.	*rt.*	Rectum.
ga.	Stomach.	*sep.*	Wall of zoœcium in the corm.
gm.	Bud.	*sol.*	Sole of the corm.
gn.	Ganglion.	*tct.*	Roof of the corm.
i.	Inner layer of bud.		

Fig. 72. Longitudinal vertical section through the peripheral part of the corm of *Lepralia Pallasiana*, showing the margin of the corm and two zoœcia, the older of which contains a polypide. × 160.

Fig. 73. Longitudinal vertical section through the margin of a corm of *Lepralia Pallasiana*, showing the two layers of this region and the origin of the polypide. × 410.

Fig. 74. Young regenerating polypide of *Flustrella hispida*. The section passes through the sagittal plane. × 380.

Fig. 75. Vertical section through margin of corm of *Flustrella hispida*, to show origin of polypide. × 410.

Fig. 76. Sagittal section through young polypide of *Flustrella hispida*, to show early stage of development of alimentary tract. × 410.

Fig. 77. Superficial view of young polypide from upper surface of corm of *Flustrella hispida*, showing young tentacles and their relation to the anus (at *atr.*). × 320.

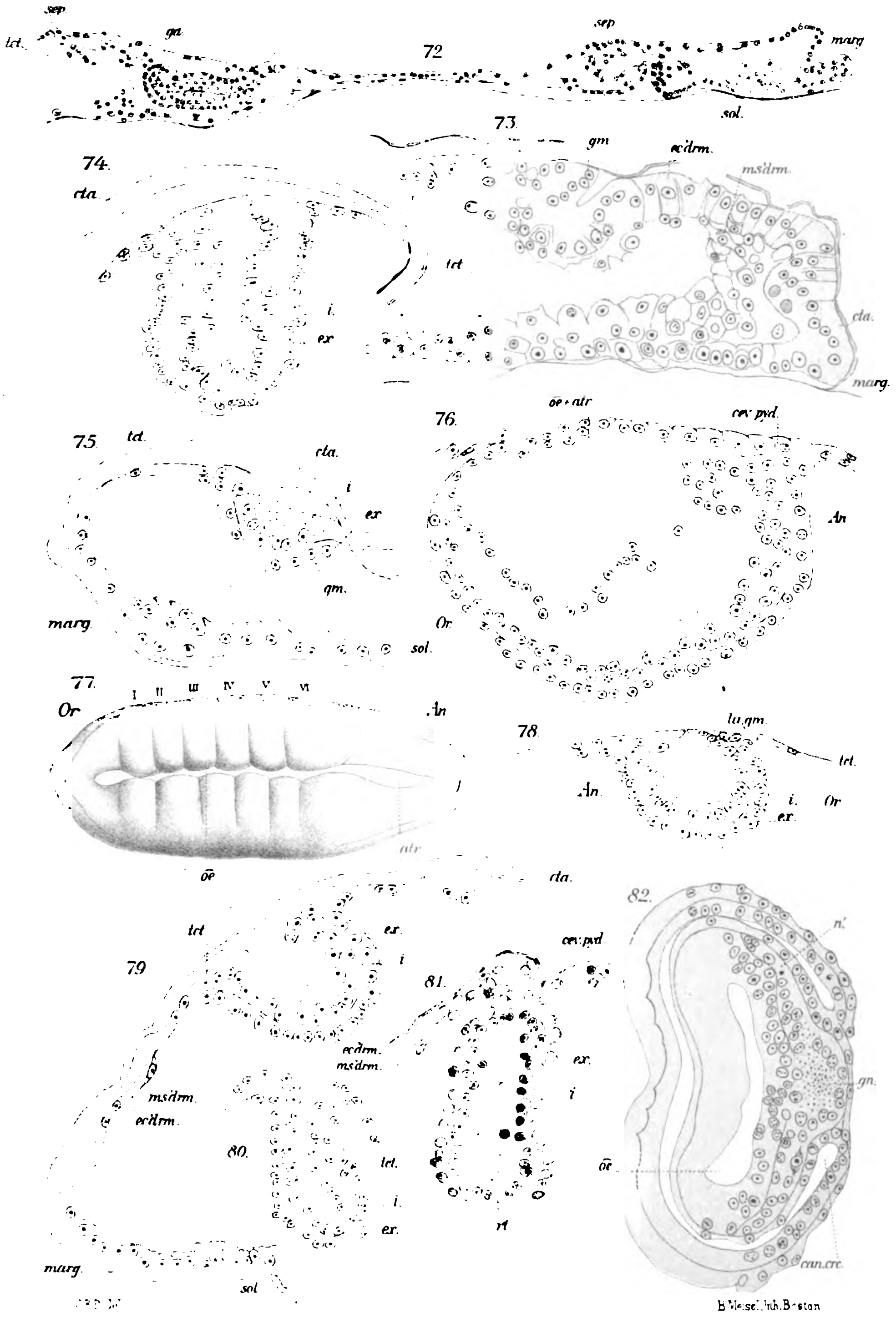
Fig. 78. Bud of polypide of *Flustrella hispida* at the time of closure of the pore of invagination. × 390.

Fig. 79. Radial section through margin of corm of *Flustrella hispida*, showing bud of polypide. × 410.

Fig. 80. Young polypide of *Flustrella hispida*. × 380.

Fig. 81. Bud of *Lepralia Pallasiana* immediately before the formation of alimentary tract, showing relation of the rectal pocket (*rt.*) to the atriopharyngeal cavity above. × 410.

Fig. 82. Section through polypide, through lately formed brain and circumœsophageal nerves (*n.'*) growing around œsophagus (*œ.*). × 410.



B. Meisel, lith. Boston

PLATE X.

ABBREVIATIONS.

An.	Anal side of polypide.	*kmp'drm.*	Kamptoderm.
an.	Anus.	*lu. gn.*	Lumen of the ganglion.
atr.	Atrium.	*ms'drm.*	Mesoderm.
can. crc.	Ring canal.	*mu.*	Musculature of œsophagus.
cev. pyd.	Neck of polypide.	*mu. ret.*	Retractor muscle of polypide.
cœ.	Cœcum.	*œ.*	Œsophagus.
cta.	Cuticula.	*op.*	Operculum.
di'sep.	Wall of zoœcium in the corm.	*Or.*	Oral side of polypide.
ec'drm.	Ectoderm.	*or.*	Mouth.
ex.	Outer layer of bud.	*pyd. dgn.*	Degenerated polypide, "brown body."
fun.	Funiculus.		
ga.	Stomach.	*rt.*	Rectum.
gn.	Ganglion.	*ta.*	Tentacle.
i.	Inner layer of bud.		

Fig. 83. Sagittal section through young polypide of *Escharella variabilis.* × 320.

Fig. 84. Regenerated polypide of *Lepralia Pallasiana* on operculum (*op.*). × 380.

Fig. 85. Cross section of pharynx of adult polypide of *Escharella variabilis*, showing perforated cell walls. × 635.

Fig. 86. Sagittal section of young polypide of *Lepralia Pallasiana*, showing formation of brain. × 320.

Fig. 87. Section parallel to sole of a corm of *Escharella variabilis* at about the stage of Figure 86, showing atrium, ganglion, and rectum. × 430.

Fig. 88. Vertical section through a bit of roof of corm of *Escharella variabilis* at neck of polypide, showing also the region of future operculum and of origin of future regenerated buds. Compare with Figure 90. × 410.

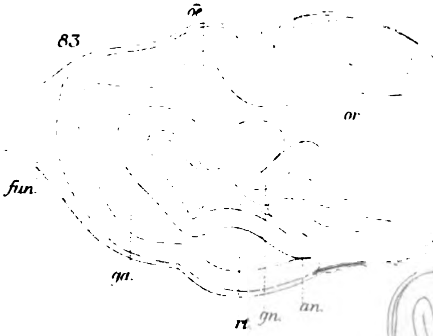
Fig. 89. Sagittal section of young regenerated polypide of *Flustrella hispida* intermediate in age between Figures 86 and 83. Shows the origin of the ganglion and rotation of the oral tentacles. × 820.

Fig. 90. Vertical section of a bit of body wall from same individual as Figure 88, to show the comparatively less embryonic condition of cells here than at neck of polypide. × 410.

Fig. 91. Operculum of *Lepralia Pallasiana* cut perpendicularly to surface, showing origin of a regenerating polypide. Body wall somewhat shrunken from cuticula. × 410.

Fig. 92. Section through a regenerated polypide of *Escharella variabilis*, showing relations of alimentary tract to "brown body" (*pyd. dgn.*). × 410.

83



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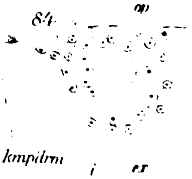

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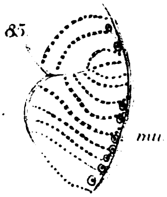

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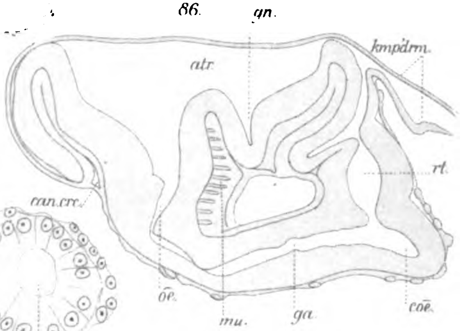

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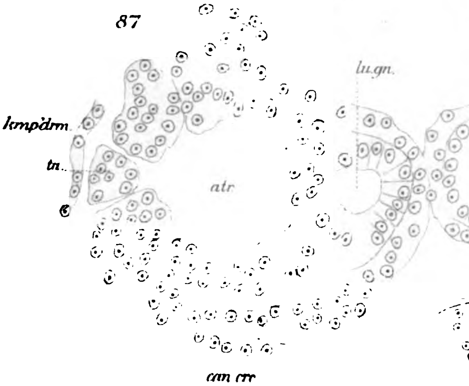

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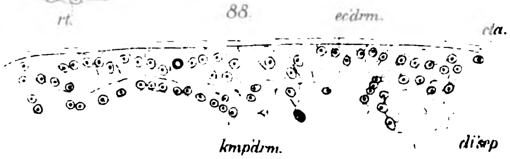

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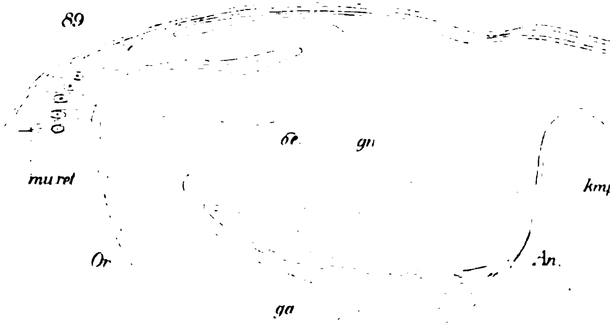

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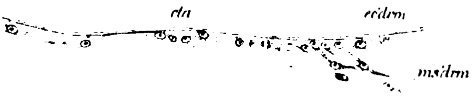

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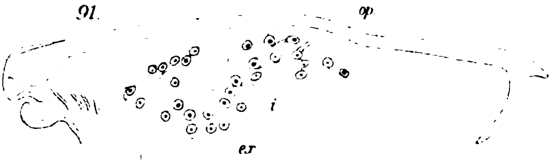

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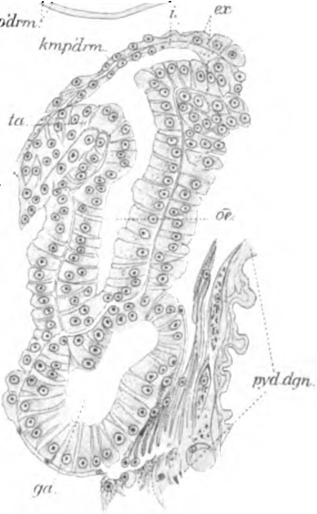


C.B.D. del.

B Meisel lith Boston

PLATE XI.

ABBREVIATIONS.

cev. oœ.	Neck of oœcium.	*ms'drm.*	Mesoderm.
cœl.	Cœlom.	*oœ.*	Oœcium.
ec'drm.	Ectoderm.	*ov.'*	Oöblasts.
en'drm.	Entoderm.	*pyd.*	Polypide.
ex.	Outer layer of bud.	*sto.*	Stolon.
i.	Inner layer of bud.	*tct.*	Roof of stock.
lu. gm.	Lumen of the bud.		

Fig. 93. A portion of a longitudinal section through a young stock of *Plumatella polymorpha*, about two weeks after hatching from statoblast (killed 12th May, 1890), showing the body wall just analward of the neck of a young polypide (*pyd.*), at the oral side of which a younger bud has already arisen. The inner (mesodermal) layer of the body wall shows oöblasts (*ov.'*) in various stages of development. × 600.

Fig. 94. Longitudinal section of oœcium of *Cristatella* showing embryo which is giving rise to the cœlomic epithelium by ingression of cells at its proximal pole, — i. e. the pole nearest the neck of the oœcium. There are in the next section two other cells in the cavity of the blastula, one of which appears degenerate in that it contains a huge vacuole, and has no distinct nucleus, the chromatic substance lying scattered loose near the cell wall. × 600.

Fig. 95. Longitudinal section through oœcium of *Cristatella* and its contained embryo. One polypide bud and the stolon (*sto.*) are shown here. There are two other buds in the embryo further developed than this one, lying to one side of it, and on the side of each of these buds is the *Anlage* of another. The *stolon* is seen to be well developed, lying between the ectoderm and mesoderm throughout the region bounded by the three older buds, and extending as a zone beyond them, and even beyond the *Anlage* of the youngest polypides. The embryonic tissue thus forms a disk about 75 × 150 μ in extent. × 390.

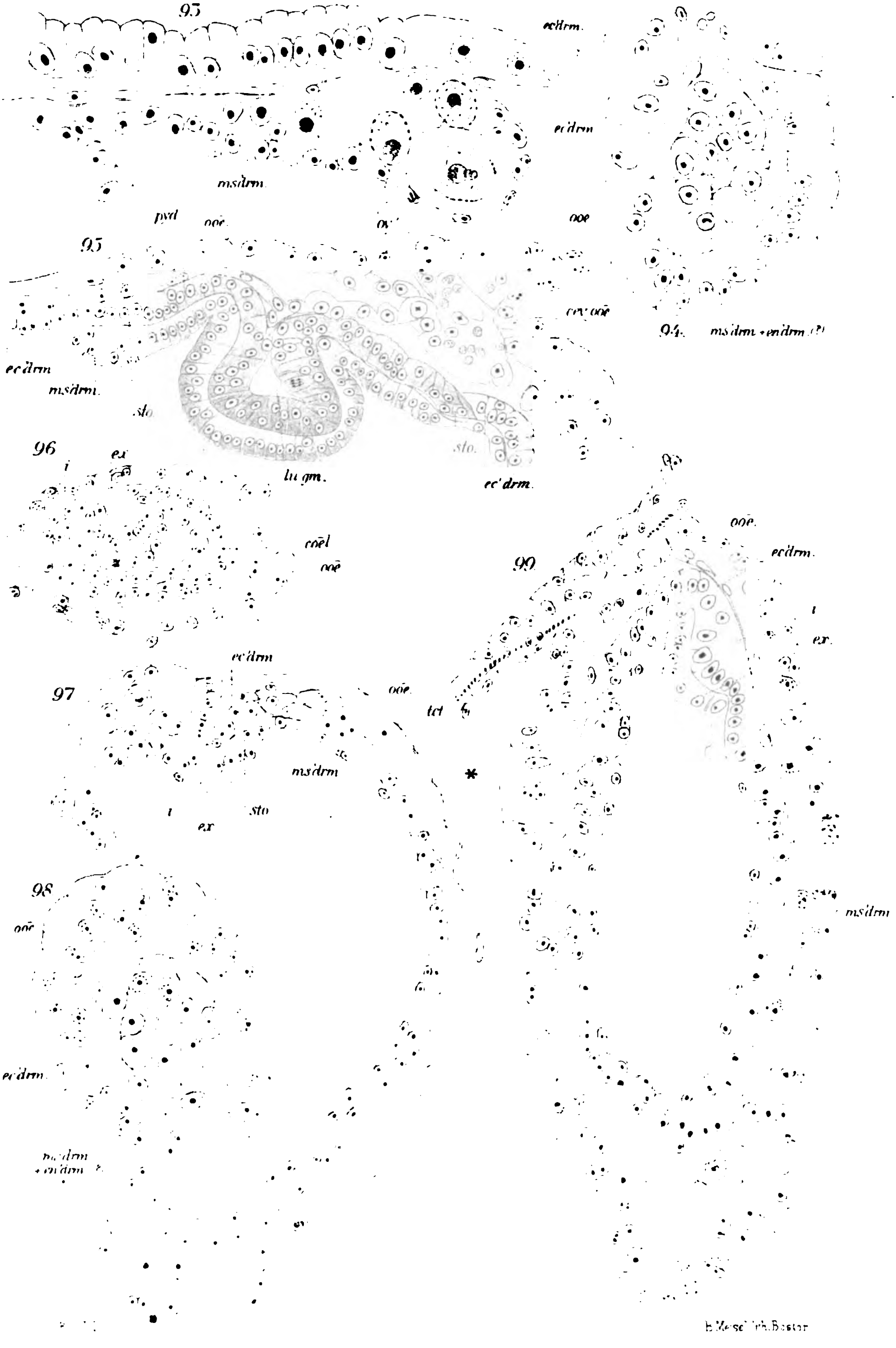
Fig. 96. Transverse section of oœcium of *Plumatella*, showing origin of first polypide. Compare with Figure 99, which represents an earlier stage. × 390.

Fig. 97. Longitudinal section through oœcium and contained embryo of *Cristatella*. The stolon is already cut off from the ectoderm. This stage immediately follows that of Figure 101, Plate XII. The forming bud is that of the first polypide. × 390.

Fig. 98. Oblique section through oœcium of *Plumatella*, showing a later stage in development of the inner layer of the larva (cf. Fig. 94). × 600.

Fig. 99. Longitudinal section of oœcium and contained larva of *Plumatella*. The bud shown at *i.*, *ex.* is the first in the colony. An incipient (second) bud is shown five sections to one side in the region indicated by an asterisk. × 410.

DAVENPORT. – BUDDING IN BRYOZOA. PL. XI.



B. Meisel lith. Boston

PLATE XII.

ABBREVIATIONS.

ec'drm.	Ectoderm.	*ms'drm.*	Mesoderm.
ex.	Outer layer of bud.	*oœ.*	Oœcium.
i.	Inner layer of bud.	*sto.*	Stolon.
lu. gm.	Lumen of the bud.		

Fig. 100. Longitudinal section of a larva of *Plumatella polymorpha*, in which the two layers are established; the pole of ingression is directed upward, on the plate.

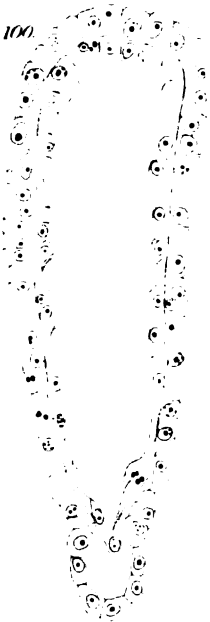
Fig. 101. Section of upper part of zoœcium of *Cristatella mucedo*, with its contained larva. Showing the formation of the stolon at the pole of ingression and the attachment of this pole to the placenta-like neck of the oœcium (*). × 390.

Fig. 102. Section through an oœcium of *Cristatella*, with its contained larva. One polypide is already established, and a second is arising. The two are the only buds in the larva. On the left of the older bud the stolon is seen to be intruding itself between the ectoderm and mesoderm of the larva. × 390.

Fig. 103. Section through the two oldest polypides of the *Cristatella* larva, together with the stolon. This larva contains one other less developed bud at one side of these two. × 390.

Fig. 104. *Plumatella polymorpha.* Stage of first bud later than that shown in Figure 96, exhibiting pore of invagination closed by overgrowth of ectoderm. × 390.

100.



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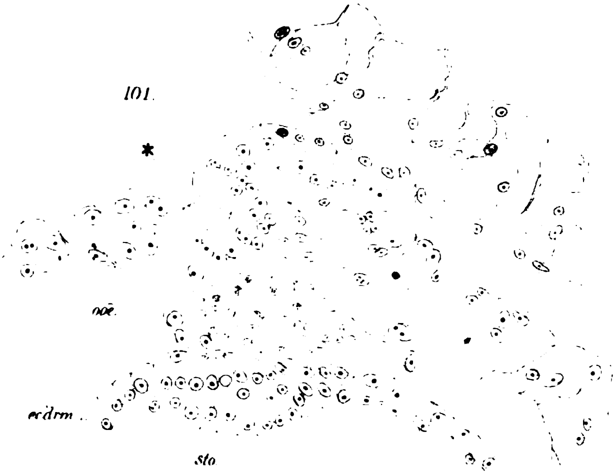

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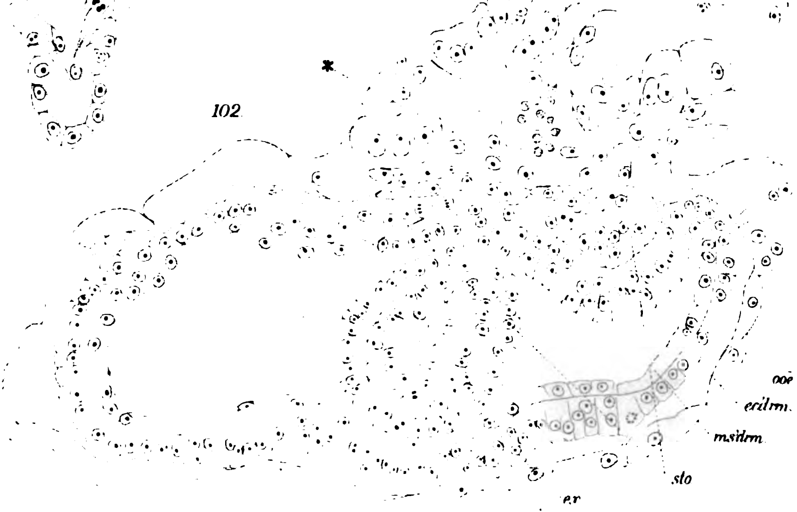

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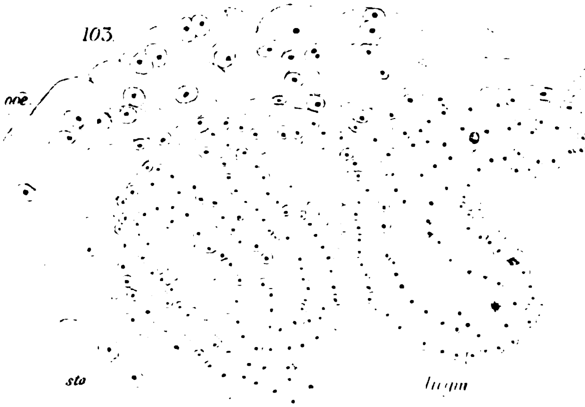

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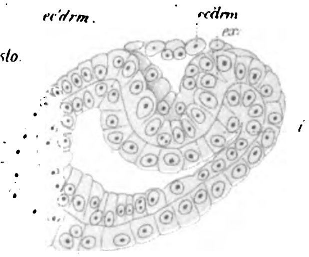

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B. Meisel lith. Boston.

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXII. No. 2.

THE GASTRULATION OF AURELIA FLAVIDULA, Pér. & Les.

By Frank Smith.

With Two Plates.

CAMBRIDGE, U.S.A.:
PRINTED FOR THE MUSEUM.
December, 1891.

No. 2. — *The Gastrulation of Aurelia flavidula, Pér. & Les.*

By Frank Smith.[1]

Preceding the appearance of Goette's ('87) publication in 1887 upon the development of Aurelia aurita and Cotylorhiza tuberculata, the gastrulation of Aurelia had been regarded, in the light of the studies of Kowalewsky, Haeckel, Claus, and others, as the result of invagination or at least of a process nearer to invagination than to any other method of gastrulation.

Goette's work seemed to show, however, that, instead of an invagination, there is an ingression of cells to form the entoderm, and that the first result of this ingression is the production of a solid gastrula, or sterrogastrula, which is only subsequently hollowed out, and is put into communication with the exterior through the formation of a prostoma at a still later period. Recently, in a paper dealing especially with the development of Cotylorhiza tuberculata, Claus ('90) reaffirms the position taken in his previous paper ('83), in which the gastrulation in Aurelia was represented as being simply a modification of invagination. In recent papers by Hamann ('90) and McMurrich ('91), Goette's views are adopted, and form part of the basis for statements that, in the development of the Scyphomedusæ, invagination, instead of being the rule, is the exception.

This want of agreement among those who have given the subject most attention makes the determination of the actual method of gastrulation in Aurelia a matter of considerable interest, and it may be assumed that any contribution to the solution of the question will not be unwelcome.

Early in the current year, at the suggestion of Dr. E. L. Mark, I undertook to investigate the method of gastrulation in A. flavidula.

Through the kindness of Mr. B. H. Van Vleck of the Boston Society of Natural History, I was enabled to spend two months of the summer of 1887 at his seaside Laboratory at Annisquam, Mass., where I then collected the material used in the present study. The embryos were killed with picro-nitric acid, and preserved in 90 per cent alcohol, in which they have been kept during the three intervening years. Of the various staining fluids tried, Erlich's acid hæmatoxylin gave decidedly the best results for sections. For examination of the whole embryos, Grenacher's alcoholic borax-carmine and Czokor's alum-cochineal each gave good results. The latter stain possesses the peculiarity of staining embryos of different ages with corresponding degrees of intensity, the youngest stages being stained the least, the degree of intensity increasing with the age of the embryo up to the planula stage.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXIX.

The result of segmentation is a one-layered blastosphere, as in A. aurita. Although the diameter of the blastocœl, or segmentation cavity, presents some individual variations at a given stage of development, it in general corresponds very nearly with that of A. aurita, as described by Goette ('87, p. 3). It increases slightly as the process of gastrulation advances. The cells of the blastosphere are usually somewhat shorter at one pole than elsewhere, and it is from this region that the entoderm is formed. The nuclei of all the cells are situated very near the outer surface of the blastosphere. Small spheroidal bodies constitute the greater portion of each cell; they are very evenly distributed through its substance, except in the vicinity of the nucleus, where they are somewhat less abundant. Vacuoles of variable sizes are usually found in some of the cells. The nuclear region stains a little more deeply than the remaining portion.

The method of gastrulation in A. flavidula is similar to that in A. aurita as described by Claus ('83, pp. 2 and 3), although it resembles even more closely a typical invagination. When the process of cleavage has resulted in the formation of a blastosphere composed of somewhat more than four hundred cells, a depression of limited extent appears in the portion of the wall which is composed of the shorter cells. From this depressed region is formed the entoderm, which develops as a single continuous layer of cells surrounding a small cavity, the cœlenteron. At the beginning of the process, and throughout its duration, the cœlenteron is in communication with the exterior by means of a narrow passage, the blastopore, or blastoporic canal. See also Explanation of Figures (Plate I. Figs. 1–4). From these figures it is apparent that only a small portion of the wall of the blastosphere is concerned in the invagination, and to that extent it must be regarded as deviating from the typical invagination, where one half of the wall of the blastosphere is infolded to form the entoderm. The cœlenteron is, however, at all stages of gastrulation, an open sac-like cavity, and therefore noticeably different from that of A. aurita, of which Claus ('83, p. 3), says: "Mit dem weiteren Nachrücken der die Mundspalte begrenzenden Zellen in das Innere des

Larvenleibes ändert sich jedoch allmählig das frühere Verhältniss zu Gunsten der Entodermfüllung, *die noch immer keine wahre Höhle, sondern eine schmale lineare, mit der Hauptachse des Leibes zusammenfallende Spalte besitzt.*"[1] With the growth of the entodermal layer, the cœlenteron enlarges, and the cleavage cavity is diminished, until finally it is entirely obliterated and the entoderm everywhere comes into contact with the ectoderm (Plate I. Figs. 4–6, Plate II. Fig. 11).

During the process of gastrulation, and also for a short time after its completion, the thickness of the entoderm, which is much less than that of the ectoderm, does not increase. Figures 5 and 6 (Plate I.) are from sections of two embryos at different stages of development. Figure 5 is from an embryo soon after the completion of gastrulation; Figure 6 is from an older stage. Since in each case the section is from the middle of its series, it follows that a decided thickening of the entoderm takes place between the stages represented by these Figures. This thickening is apparently due to an increase in the number of the cells, which are soon unable to find room for themselves except by elongation. The entodermal cells are quite different in appearance from those of the ectoderm; they are approximately spherical, and do not have as numerous spheroidal yolk bodies as the latter. Their nuclei, however, closely resemble those of the ectoderm, and usually lie in the portion of the cell nearest the cœlenteron.

As is to be seen from Plate II. Fig. 7, — a section nearly perpendicular to the blastoporic canal, — the blastopore in A. flavidula is very small. A similar condition has been shown by Claus to exist in A. aurita, and by Metschnikoff ('86, Taf. X. Fig. 14) in Nausithoë marginata.

The nuclei of the cells composing the wall of the blastosphere are situated, as has been stated, near the surface of the sphere. But at about the time of the beginning of the invagination, sometimes a little earlier, a few of the nuclei are found in the deeper portion of the wall. At first there are only one or two such displaced nuclei to be observed in the whole embryo, but as development progresses they increase in number. A careful examination of sections shows that the cells to which they belong do not extend, like the remaining cells of the wall, through its whole thickness, but that they are wedged in as it were between the bases of the ordinary cells. The latter are much elongated, and from mutual pressure are prismatic, whereas the deep cells are spheroidal and project in some cases into the segmentation cavity. Since these cells are found at various intermediate positions between the outer and inner surfaces of the wall, I infer that they result from a process of migration inward, either at the time of cell division or independently of that process. Indeed, there is obviously no other possible source whence these cells could come, but the exact process of transfer is not easily determined. I believe that this increase in number is at first for a considerable time due exclusively to the migration of cells which once shared in forming the external boundary of the sphere, but later the division of cells which have already migrated into the deeper portion of the ectoderm undoubtedly contributes to this increase.

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[1] The original is not Italicized.

We have now to turn our attention to a phenomenon of considerable importance, the study of which from preserved material is, however, attended with difficulties. I refer to the ingression of cells from the wall of the blastosphere into the cleavage cavity, which begins a considerable time before the invagination commences. The latter does not take place until the number of cells forming the wall of the blastosphere has exceeded 400, whereas the ingression, as far as can be inferred from the cases which I have studied, may occur at any time after the blastosphere contains about 100 cells up to the period of invagination. The phenomenon of ingression in A. flavidula is not of constant occurrence, but when it does take place is similar to that represented by Goette ('87, Taf. I. Figs. 1–5) for the earlier stages of the blastula in A. aurita. It consists of a migration into the cleavage cavity of one or two, rarely more than three, of the cells of the blastospheric wall. With the exception that they assume a spherical form, because relieved from pressure, they are at first similar in size, as well as in nuclear and other characters, to the cells remaining in the wall.

The study of ingression upon preserved material is attended with difficulty, since in any one specimen we have the condition at only one stage of development, and cannot say with certainty what its condition has been in past stages, or what it might have been during some subsequent period. This can be determined only by studying the conditions existing in other embryos killed at other stages, and arranging all in their probable natural sequence. In view of this fact, I have sectioned and examined several hundred embryos which were killed at different stages of development. As far as possible the results obtained from these sections have been verified by the study of embryos cleared and mounted whole. Although this ingression occurs before invagination, I have deferred the discussion of it until now, because invagination is constant in its occurrence, whereas the ingression does not appear to be so; indeed, the majority of the specimens have shown no indications of it.

The subsequent history of these cells, as shown by the comparison of specimens of succeeding stages of development is both interesting and peculiar. I imagine that it is such cells as these to which Claus ('90, p. 3) refers when he says: "Ich habe den vereinzelt eingetretenen zwei bis drei Zellen, weil sie nicht regelmässig in jeder Blastula sich ablösen, der am vegetativen Pole einwuchernden Zellenmasse gegenüber keine weitere Bedeutung beigemessen, so dasse ich dieselben zwar auf einer Abbildung darstellte, im Texte aber nicht besonders erwähnte, und bin auch jetzt noch der Ansicht, dass diese auffallend kleinen Zellen wieder rückgebildet werden und überhaupt nicht zur Bildung des Entoderms beitragen." In my judgment, a part of the difference of opinion between Goette and Claus is due to the fact that there are two kinds of cells which find their way into the cleavage cavity. These are the large cells described by Goette as beginning to be formed at an early stage of the blastula, and much smaller cells, of which I shall have more to say hereafter, that make their appearance only at later stages of development. Claus seems to have seen "very small cells," and to have assumed that they were equivalent to the large cells figured by Goette. I am unable to say with certainty that the cells seen by Claus are the equivalents of those figured by Goette, but Claus assumes that they are, and I have the more reason to believe it because the large cells are of more frequent occurrence than the small ones. But if this be so, I do not understand how Claus could speak of them as "diese auffallend kleinen Zellen." But however that may be, I have reason to believe that the supposition of Claus, that they ultimately degenerate, is correct.

Soon after the ingression of a cell its nucleus undergoes changes which result in its disappearance as such, for instead of a nucleus there can be seen only one or more small, isolated, deeply stained particles, which I judge to be scattered portions of the nuclear chromatine (Plate II. Figs. 8 and 10). Even these are often wanting. I have said that this nuclear change follows soon after the ingression of the cell, because out of the numerous instances in which these cells have been present there is not one in which the nucleus retains its original condition after the cells in the wall of the blastula have given evidence, by their diminished size, that they have undergone division since the ingression took place. This conclusion is in part based on the assumption that at the time of ingression the ingressing cells are of about the same size as those which remain in the wall of the blastula. The ingressing cells sometimes persist, without any further apparent changes than the disintegration of the nucleus, until the process of gastrulation is completed. Such cases are not as common, however, as others, where there is to be found in the cleavage cavity material which appears as though it had resulted from the disintegration of similar cells. This material has a spongy or vacuolated appearance, and contains faintly staining bodies or granules similar to those found in the ectodermic cells; it does not possess definitely circumscribed boundaries; on the contrary, it fills the cleavage cavity more or less completely, but is not of uniform density throughout. The fact that this material is not homogeneous, and that it contains granules, etc., prevents the conclusion that it has been produced as a simple secretion into the cleavage cavity, although it may have been formed in part by such a process. The frequent association of this material with ingression cells in the same specimen (Plate II. Fig. 8), and the lack of other ways of accounting for its presence, lead me to believe that it is produced by the disintegration which I have suggested.

There is another peculiarity of the development which I believe to be connected with this process of nuclear disintegration. It is this: after having once entered the cleavage cavity the immigrating cells seem to lose their power of division, and consequently do not become more numerous, while the cells composing the blastospheric wall undergo repeated divisions, as is shown by their increased number and diminished size.

The number of these immigrating cells is small, usually only one or two, very rarely more than three, so that I have not been successful in finding the "Verbindungsglieder" connecting the conditions shown by Goette ('87, Taf. I.) in his Figures 5 and 6, which Claus ('90, p. 4) regarded as essential to the substantiation of Goette's view of the method of gastrulation.

Reference has been made to the fact that in some cases the ingrowing cells persist both during and after the process of invagination. In the latter case, they are to be found in the cœlenteron rather than in the cleavage cavity. Figure 11 (Plate II.) is drawn from such a specimen. Figures 9 and 10 represent two sections of one individual in which the invagination is not completed, and furnish a hint as to the process by which the cells pass into the cœlenteron from the cleavage cavity. The entoderm being composed of less closely fitting cells than the ectoderm, doubtless admits the passage of the large immigrated cells through it more readily than the latter would (Plate II. Fig. 9). The immigrated cell is of course passive in this process. Since it is prevented by the firm wall of the ectoderm from escaping, the pressure exerted upon it by the enlarging entoderm is probably sufficient to cause it to be forced through the entodermic wall into the cœlenteric cavity. From Figure 10 it is to be seen that one cell has already reached the gastral cavity. In speaking of these peculiarly situated cells I have thus far assumed that they are such as originally reached the cleavage cavity by an early ingression, where, with changed nuclear condition, but apparently with no further alteration, they have remained until the time of gastrulation. That this is their source is evident from the following considerations. First, the small diameter of the blastoporic canal (Plate II. Fig. 7), which is from the same series as Figures 9 and 10, precludes the assumption that they might have entered the gastrula cavity from without. Secondly, in their large size and general appearance they are unlike the cells of either ectoderm or entoderm at any time during gastrulation, and so could not have been derived from those sources during that process. Thirdly, they do correspond in size and general characters, except in their nuclear conditions, with the cells of the blastospheric wall as the latter appear at the time when ingression takes place.

It is difficult to state either the cause or the purpose of this immigration. That it is not essential to the welfare of the embryo, either by affording nourishment to the developing cells of the entoderm, or in any other way, is evident from the fact that in a large number of cases it does not occur. That it is not an inherited tendency, derived from a more primitive method of gastrulation by ingression, is probable from the fact that the immigrating cells do not appear to have any share whatever in the formation of the entoderm. On the other hand, its occurrence seems to be much too frequent to be considered as accidental.

I have stated previously (p. 119) that two very different kinds of cells are to be found at times in the cleavage cavity. Besides the large immigrating cells already described at length, I have found in a much smaller number of cases very small cells (Plate I. Fig. 2), one or two in number, that appear precisely like the deep-lying ectodermal cells already described. Because of their strong resemblance to the latter, their exceptional occurrence, and the fact that they do not appear until after the beginning of the development of the deep-lying ectodermal layer, I incline to the opinion that they are derived from that layer, and that their occurrence is entirely accidental.

At first it appeared to me surprising that two investigators could reach such different conclusions as those published by Claus ('83 and '90) and Goette ('87), concerning the method of gastrulation in the same animal, A. aurita. Since studying this process in A. flavidula, it seems less strange. The results obtained from my first sections led me to think that the conclusions reached by Goette would be confirmed in the case of A. flavidula. Better staining, thinner sections, and more accurate orientation have made it certain, however, that the method of gastrulation in this species is much more in accord with the description given by Claus, and that the process really is one of invagination.

Certain considerations weaken my confidence in the position defended by Goette. A comparison of his Figures 6–9 ('87, Taf. I.) with some of my thicker sections, or with those which were made when the gastrula was so oriented as not to be cut parallel to the blastoporic canal, makes it appear to me probable that his results are based upon similar inadequate sections. In Figure 8 (Plate II.) there are only about one half as many nuclei visible as there are cells, the nuclei of a portion of the cells being contained in adjacent sections. In figures of corresponding stages of A. aurita as represented by Goette ('87, Taf. I.), nuclei are figured in *nearly all the cells.* I believe this to be evidence that his figures were drawn from *thick* sections. The blastopore, because of its very small diameter, is quite easily overlooked in thick sections, and especially if the plane of sectioning is somewhat oblique to the longitudinal axis of the blastopore. Since, as previously stated, the nuclei of the entodermal cells are usually situated in the portion of the cell nearest the cœlenteron, it is easy to find in thick sections of an invaginating embryo conditions like those represented by Goette in his Figures 6–8. My Figure 12 (Plate II.) reproduces a section of the same series as that represented in Figure 3 (Plate I.). The intervening section (not figured) is quite similar to Goette's Figure 8. An examination of the cells bordering the blastoporic canal in Figure 3 will show how sections like Figure 12, or such as are a little oblique to the chief axis of the embryo have the appearance of containing immigrating cells. Such sections also exhibit the flattening in the region of the shorter cells to which Goette ('87, p. 4) has called attention in the following words: "Schon während der Gastrulation zeigt sich eine Stelle des Keims im Bereich seiner kürzeren Zellen etwas abgeplattet."

Additional considerations increase the probability of the correctness of the view which I have advanced to explain Goette's error. With advancing stages of development, I have found an increase in the number of the cells composing the ectodermic wall. This is undoubtedly subject to slight individual variations, but the number of such cells is nevertheless in quite close correlation with the stage of development. An examination of Goette's Figures 6–9 ('87, Taf. I.) reveals such a similarity in the number and size of the cells composing the ectoderm in each of the four supposed stages, that I am driven to the conclusion that they represent sections from specimens of a single stage of development, which may have been produced by cutting in planes having different relations to the chief axis of the embryo.

When we consider that in the majority of embryos there are no signs of ingression, and that in the cases where it does occur the immigrating cells in some instances degenerate early, and in others persist undivided throughout the process of gastrulation, and that they at no time show evidences of even sharing in the formation of an entoderm, — and when we further reflect that all the conditions shown in Goette's Figures 6–9 can easily be reproduced from sections of invaginating gastrulæ of a single stage of development, — it seems improbable that the entoderm of Aurelia develops even occasionally by ingression. At present, therefore, there seems to me to be no evidence that in this genus gastrulation occurs by both methods, invagination and ingression.

The Scyphomedusæ present several interesting variations in gastrulation. The anomalous development occurring in Lucernaria is as far removed from the usual process as that group itself is from the other Scyphomedusæ. According to McMurrich ('91, p. 314), the solid planula in Cyanea arctica is formed by the immigration of certain of the blastula cells. This planula is subsequently hollowed out, and gives rise to a structure like an invaginate gastrula, but it is formed without any invagination. In Cyanea capillata (Hamann, '90, pp. 16, 17) there seems to be a solid ingrowth of cells from one pole of the embryo, and a simultaneous development of the cœlenteron. The entoderm of Chrysaora (Claus, '83, p. 5, Taf. I. Fig. 21 *h*) is developed in a way which is somewhat similar to that described by Hamann for Cyanea capillata. According to Claus ('83, p. 2, and '90, p. 4), the gastrulation of Aurelia aurita approximates the method by invagination a little more closely than that of Chrysaora, since its cells are arranged in a single layer about the fissure-like cœlenteron. Aurelia flavidula exhibits a still more nearly typical invagination, since the cœlenteron is from the beginning an open sac-like cavity. Cotylorhiza tuberculata (Cassiopea Borbonica) has an invaginate gastrula which closely resembles that of Aurelia flavidula (Claus, '90, Taf. I. Figs. 2 and 3; Kowalevsky, '73, Taf. II. Fig. 1). Finally, in Pelagia noctiluca and Nausithoë marginata, as shown by Metschnikoff ('86, pp. 66–68, Taf. X.), there is a typical invagination.

If the observations of McMurrich ('91, p. 314) on Cyanea arctica are substantiated, we have among the Scyphomedusæ one example of the formation of a sterrula by ingression, with the subsequent formation of a gastrula-like structure, without an invagination. From the preceding summary it is to be seen that there are in Scyphomedusæ two cases in which the mode of gastrulation appears to be intermediate between ingression and invagination, and at least four cases of unquestionable invagination. If, in the light of so much variation in the mode of gastrulation in this group as is shown by the few forms studied, it is safe to conclude that any one mode is typical, that mode would certainly appear to be invagination, and not, as Hamann and McMurrich have recently maintained, ingression.

CAMBRIDGE, June 20, 1891.

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EXPLANATION OF FIGURES.

All the figures were drawn from sections with the aid of an Abbé camera. The sections from which the figures were made were 5 μ in thickness.

PLATE I.

ABBREVIATIONS.

bl'po.	Blastopore.
cav. sg.	Segmentation cavity.
cl.	Immigrated cell.
cœlent.	Cœlenteron.
cog.	Coagulum.
ec'drm.	Ectoderm.
en'drm.	Entoderm.
nl.	Chromatic portion of degenerated nucleus.
nl. ec'drm.	Nuclei of deeper portion of ectoderm.

Figures 1–4. Sections to illustrate the nature of the invagination.

Fig. 1. An early stage of invagination. × 460.

" 2. A slightly later stage than that of Figure 1. × 540.

" 3. A stage in which the invagination is well advanced. × 385.

" 4. A gastrula with invagination completed. × 410.

" 5. Section of a gastrula cut in a plane (equator) perpendicular to the axis of the blastoporic canal. × 385.

" 6. Section of an older individual through the equator, showing increase in thickness of the entoderm. × 385.

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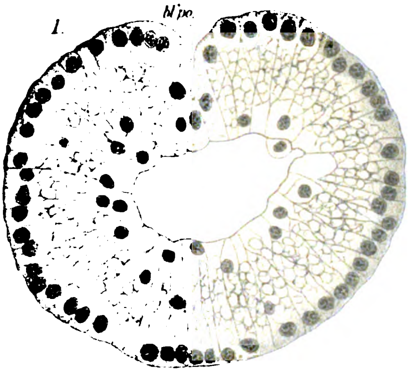

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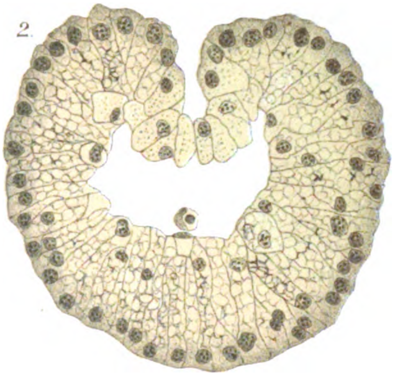

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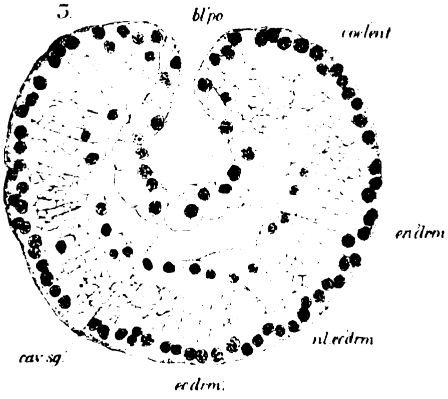

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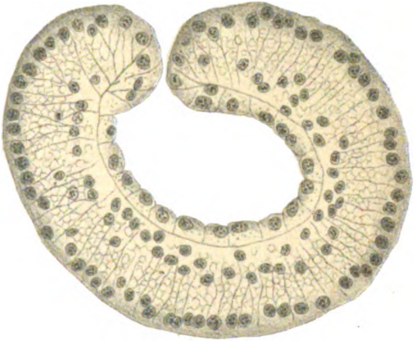

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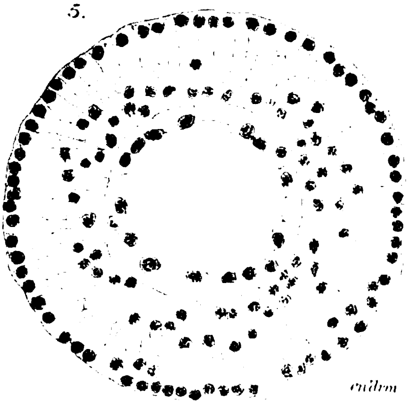

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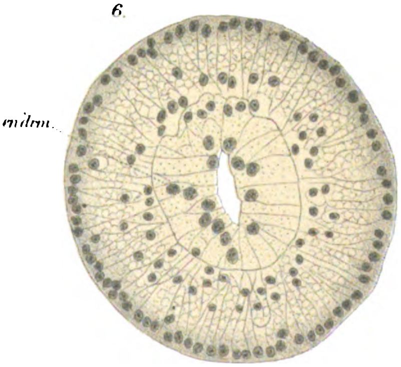

F. S. del.

B. Meisel lith. Boston.

PLATE II.

ABBREVIATIONS.

bl'po.	Blastopore.
cav. sg.	Segmentation cavity.
cl.	Immigrated cell.
cœlent.	Cœlenteron.
cog.	Coagulum.
ec'drm.	Ectoderm.
en'drm.	Entoderm.
nl.	Chromatic portion of degenerated nucleus.
nl. ec'drm.	Nuclei of deeper portion of ectoderm.

Figures 7, 9, and 10 are from different sections of the same individual.

Fig. 7. Section through the blastoporic canal and nearly perpendicular to it. × 410.

" 8. Section at a stage preceding invagination. It shows an immigrated cell in which the nucleus has degenerated. × 385.

" 9. Section before the close of gastrulation, showing an immigrated cell in the segmentation cavity. × 410.

" 10. Section from the same individual as Figure 9. It contains an immigrated cell in the cœlenteric cavity. × 410.

" 11. Section of a gastrula with two immigrated cells contained in the cœlenteric cavity. × 385.

" 12. Section from the same individual as Figure 3, to show the appearance when the gastrula is cut parallel to, but at one side of, the blastoporic canal. × 385.

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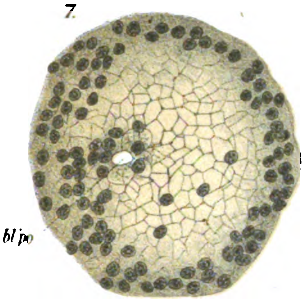

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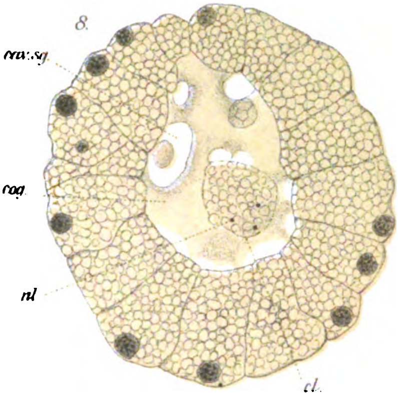

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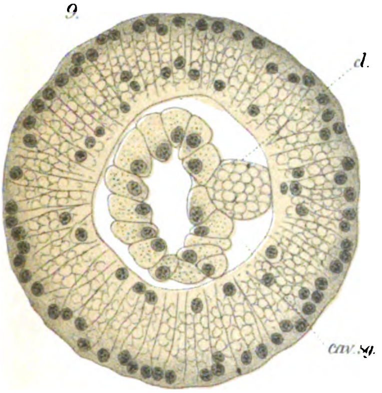

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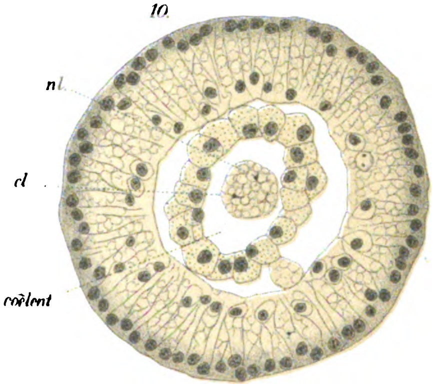

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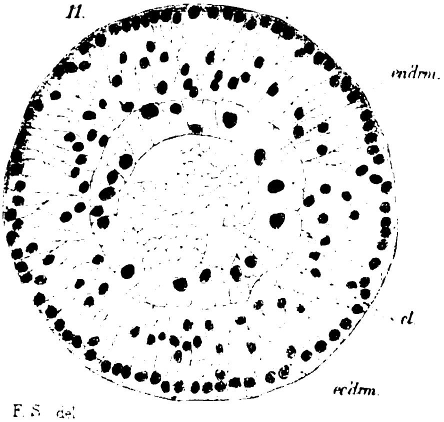

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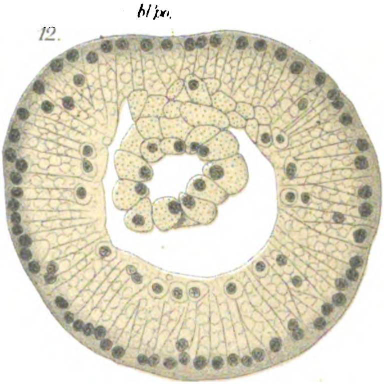

F. S. del.

B. Meisel lith. Boston

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AMITOSIS IN THE EMBRYONAL ENVELOPES OF THE SCORPION.

BY H. P. JOHNSON.

WITH THREE PLATES.

CAMBRIDGE, U. S. A.:
PRINTED FOR THE MUSEUM.
JANUARY, 1892.

No. 3.—*Amitosis in the Embryonal Envelopes of the Scorpion.*

By H. P. Johnson.[1]

In the fall of 1889, at the suggestion of my instructor, Prof. E. L. Mark, I decided to work upon the problem of the so-called "direct" or amitotic division of nuclei. While in search of suitable material, my attention was called to a brief article by Blochmann ('85), describing a very well marked amitotic division for the large nuclei of the embryonal membrane of the scorpion. A number of *Centrurus* embryos were kindly given to me by my friend, Dr. G. H. Parker. These embryos had lain in 90% alcohol since the summer of 1886. The mode of fixation (for the purpose of studying the development of the eyes) was somewhat unusual; for, immediately after their removal from the mother, they were immersed in 35% alcohol, and thence carried up quite rapidly, through 50 and 70%, to 90%. Notwithstanding this rather crude method, the membranes were in excellent histological condition, in no way inferior to material afterwards prepared by the most approved methods of fixation.

In addition to the material above mentioned, I received from Mr. Richard Goeth, of Burnet County, Texas, during the following winter and spring, about three dozen live specimens of *Centrurus* (sp. incog.).[2] A lot that arrived in the latter part of May contained several pregnant females, with embryos in different stages. The scorpions were chloroformed, and the ovarian tubes with the embryos enclosed were dissected out as quickly as possible. A number of killing agents were used, including Flemming's weaker chrom-aceto-osmic, Rabl's chrom-formic, Perenyi's fluid, Kleinenberg's picro-sulphuric, and Merkel's fluid.

For staining, I have used chiefly Ehrlich's hæmatoxylin. Grenacher's alcoholic borax-carmine and Czokor's alum-cochineal have given fair results. Safranin, employed according to Flemming's method, I have found less serviceable than the stains above mentioned. After staining, the preparations were dehydrated, cleared with oil of cloves, and mounted in benzole-balsam.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXX.

[2] This is the species used by G. H. Parker in his study on the development of the eyes (see Bull. Mus. Comp. Zoöl., Vol. XIII. No. 6, p. 173, 1887), and was then undescribed. I am not aware that it has since received a name.

The embryo is enveloped by three epithelial membranes, the ovarian capsule, the *membrana serosa*, and the amnion, — named in order from without inward.

The serosa and amnion are strictly embryonic structures, analogous to the fœtal membranes of the higher Vertebrates. There are two contradictory accounts as to the manner of their formation. Possibly they do not arise in the same way in all genera of scorpions. In a brief communication by Kowalevsky und Schulgin ('86, p. 526) upon the development of *Androctonus ornatus*, it is stated that they originate as a fold from the edge of the blastoderm, the outer layer of the fold forming the serosa, the inner the amnion. The fold grows up over the blastoderm, the edges coalesce, and the membranes finally separate from the ovum. The more recent account by Laurie ('90, p. 114) states that in *Euscorpius* the serosa arises by a proliferation of the peripheral cells of the blastoderm, extends as a delicate membrane forward and backward over the egg, which it finally covers completely, and then becomes entirely separate from the blastoderm. The formation of the amnion begins when the serosa has covered about two thirds of the embryo, and, like the serosa, its origin is ectodermic. The amnion, however, "never loses its connection with the epiblast as the serous membrane has now done, but remains attached to its edges and only extends round the egg as the epiblast extends" (p. 116). Unfortunately, I have not obtained sufficiently early stages of *Centrurus* to ascertain how its membranes arise, but, in removing the latter from the embryo, I have never found the amnion attached to the ectoderm. The membrane which I have called the "ovarian capsule" I at first wrongly took to be the follicular epithelium, and under this supposition it was indicated as *e'th. fol.* in Figure 2. Like the follicular epithelium, it arises from the ovarian tube; but the follicle is formed as a diverticulum of the tube, previous to the maturation of the ovum, and serves as a nutritive capsule for the latter during its growth. The ovarian capsule, on the contrary, is that part of the ovarian tube which receives the ovum after fertilization, and enlarges to accommodate the growth of the embryo.

The fœtal membranes fit so loosely over the embryo that they can be easily removed in a single piece. In late stages, the ovarian capsule is readily separable from the membranes; in earlier stages, it adheres closely to them. It is rarely possible to separate the serosa from the amnion, and a transverse section (see Fig. 2) shows only a trace of a dividing wall between them, although in surface view the cell walls of both membranes are clearly seen (Fig. 1). Metschnikoff (71, p. 219) describes the membranes of *Scorpio* (*Euscorpius*) *italicus* as connected with each other by delicate fibres, which terminate just over the amniotic nuclei. I have found such fibres in the earlier stages of my material, but not in the older ones, nor are they everywhere present in the younger membranes. The membranes of the Brazilian scorpion examined by Blochmann ('85, p. 481) were found closely applied to each other.

I. The Serosa.

Plate I.; Plate II. Figs. 14, 15; Plate III.

The cells of the serosa have great superficial extent, measuring half a millimeter or more in diameter; but proportionally they are very thin. Their size is exceedingly variable, as may be seen by comparing Figure 3 with Figures 11 and 13 of the same magnification, although the last two represent cells of only average size. Both small and large cells are apt to be aggregated in certain parts of the serosa, yet very small cells often occur sporadically in the midst of large ones. The cell walls are extremely distinct in late stages of the embryo, but in earlier stages are often difficult to trace in an ordinary stained preparation. As remarked by Blochmann, they have a distinct fibrous structure. The cells are irregularly polygonal in shape, usually elongated, sometimes nearly square or triangular. Not infrequently they are bounded by curved outlines (Fig. 13).

The nuclei of the serosa measure from $25\,\mu$ to $60\,\mu$ or more in diameter, but as a rule are small in proportion to the cells (Figs. 1–3 and 11–15). In the membranes of young embryos the nuclei are larger absolutely and in proportion to the cells than in old membranes. In face view the resting nucleus is nearly circular; in section, it is seen to be considerably flattened, in accordance with the thinness of the cell (Fig. 2, *nl. sr.*). It occupies the full thickness of the serosa, and sometimes causes a bulging of the cell at the point where it lies, as is shown in Figure 2. Blochmann states ('85, p. 480) that the nuclei of the serosa always cause that membrane to encroach *inward* upon the amnion; but a dividing line between amnion and serosa is so seldom visible in *Centrurus*, that I am unable to say whether such is the case.

The nuclear membrane is thin, but clearly visible, except in nuclei that have undergone degeneration. The chromatic substance, or nuclein, is for the most part in the form of granules distributed evenly throughout the nucleus. Indications of a reticular or filamentous structure are, however, frequently present. I believe there is a chromatic network throughout the nucleus, but the abundance of granular chromatin prevents one from tracing it. Several nucleoli are always present. They are extremely variable in size and shape, and in many cases appear to be only aggregations of granular chromatin. They take a stain with hæmatoxylin and carmine in no way different from the rest of the chromatin, except that it is more intense.

A very large proportion (about four to one) of the cells of the serosa contain two nuclei. These pairs of nuclei have all arisen from single nuclei by amitotic division. It is obvious that division of the cell is not contemporaneous with, and does not immediately follow, the division of the nucleus. In many cases, especially when the embryo is far advanced, cell division probably does not occur at all. Very few cells out of the thousands I have examined have had more than two nuclei; but I have found several with three nuclei, and two cells with *four*. This seems to be the maximum number. These cells of the serosa, therefore, are not to be classed with multinucleate cells in which the nucleus divides into a great number of irregular and unequal fragments. Here the division takes place in an orderly fashion, and division of the cell follows nuclear division in regular sequence, though not immediately.

In every serosa examined, nuclei were found in process of division. Some preparations furnish many more examples of division than others; and occasionally three or four adjacent cells will contain dividing nuclei (Fig. 15). Very frequently, however, only one or two dividing nuclei will be found in the whole serosa. It cannot therefore be supposed that nuclear division is frequent; and I have found that there are more cells with dividing nuclei in the membranes of late stages of the embryo than in the earlier ones.

The first sign of approaching division is an elongation of the nucleus (Fig. 4), almost always parallel to the long axis of the cell. Naturally, the elongation progresses by insensible gradations from the nearly circular form of the resting nucleus, so that one cannot say positively that the nucleus is going to divide until the elongation has become marked. The absolute amount of elongation varies greatly, and is less in the membranes of young embryos than in those of older ones. The example represented in Figure 4 is from an old membrane, and shows almost the extreme of elongation. This stage, while giving not the slightest evidence of ordinary mitosis, is characterized by a longitudinal arrangement of the chromatic substance, as indicated in Figure 4. The effect is most marked upon the nucleoli. Blochmann ('85, p. 482) found only two nucleoli at this stage, and these were usually situated one at each end of the elliptical nucleus. Where there are several nucleoli, as is usually the case with the nuclei I have studied, there is an approximately equal distribution of them to the daughter nuclei. The nucleoli vary so much in size and shape, that it is impossible to say how precise is the apportionment of chromatin by this method.

Most nuclei in the elongated condition already show a slight constriction, generally more marked on one edge than on the other (Fig. 4). If no further elongation takes place, the constriction becomes deep and narrow, as represented in Figures 5 and 12. This style of division is characteristic of young membranes, and gives rise to daughter nuclei which lie close together, or even in contact (Fig. 13). It is doubtless a more vigorous and rapid type of division than that found in the older membranes, to be described directly. If the nucleus continues to elongate while constricting, it assumes the dumb-bell form represented in Figures 6 and 7. The daughter nuclei, at first ovate or pyriform, become rounder as the connecting thread becomes thinner. Division of this type is almost confined to old membranes; I have rarely found it in those from young embryos.

The nuclei represented by Figures 6 and 7 show more clearly than usual a peculiar arrangement of the chromatic threads. The filaments have the appearance of a fascicle of slender rods, which lie very close together in the connecting bridge, and thence radiate into both daughter nuclei. They are stainable both with carmine and hæmatoxylin. Sometimes these threads can be resolved into rows of granules (Fig. 7, right-hand daughter nucleus). The later stages also show traces of these longitudinal threads (Figs. 8, 9, 10). In the example represented by Figure 6, the nucleoli partook of the general longitudinal disposition of the chromatic substance, but were probably arranged in this manner at an earlier stage of division, as explained for Figure 4. In the later stages of division, this arrangement of the nucleoli is gradually lost.

The final stages, represented in Figures 8, 9, 10, may be briefly described. These stages are far commoner than the early ones; hence, it must be supposed that they require more time. The constricted portion is drawn out into a thin, deeply staining thread. This thread undoubtedly contains chromatin, and in a peculiarly condensed form. In this respect these nuclei differ from the nuclei of the Malpighian vessels of *Aphrophora spumaria*, as described and figured by Carnoy

('85, Plate I. Fig. 7); for the connecting thread in the dividing nucleus of *Aphrophora* remains unstained, and therefore contains no chromatin.

The dividing nucleus represented by Figure 8 is peculiar in several respects. In the first place, the daughter nuclei are very unlike in form, though this is by no means unusual with dividing nuclei from old membranes. All the stainable nucleoli are in one daughter nucleus, while the other still shows a faint longitudinal arrangement of its chromatic threads. The sharply stained connecting thread is notched at a point midway between the daughter nuclei, probably indicating the place where, at a later stage, rupture would have occurred. The daughter nucleus on the left is nearly destitute of chromatin in the crescent-shaped space lying next the connecting thread, and an inner contour line is visible (x), from the central point of which a stainable cord extends to the proximal end of the connecting thread. I have seen a similar appearance in the late stages of other dividing nuclei, and it undoubtedly indicates the manner in which the daughter nuclei sometimes attain a rounded form. Occasionally, however, daughter nuclei entirely separate from each other have a conical or tapered form.

In the last stages of division, the connecting thread is drawn out to extreme tenuity (Figs. 9 and 10). So exceedingly fine does this thread become, that, with the highest power accessible to me (Zeiss's homogeneous immersion objective $\frac{1}{18}$), I could barely trace its course through the cytoplasm, though in most cases I made out that it was continuous from nucleus to nucleus. It is finally broken at or near the centre, and the proximal tips, as Blochmann suggests, are probably absorbed by the daughter nuclei. In even so late a stage as that shown by Figure 10, the longitudinal chromatic filaments are still perceptible. The right-hand daughter nucleus contains four loop-shaped bodies that strongly resemble chromosomes. They are, however, almost unstained by hæmatoxylin.

Blochmann states ('85, p. 482) that in no case did he find a division of the cell following the division of the nucleus. As already said, the great proportion of binucleate cells renders it certain that cell division is not an *immediate* consequence of nuclear division. Although I have carefully examined great numbers of binucleate cells, I have only once seen a cell wall in process of formation (Fig. 27). Yet one finds plenty of evidence that cell division does take place. Pairs of cells like those in Figure 11 are of frequent occurrence. It is safe to infer, I think, from the arrangement of the binucleate cells which surround these, as well as from the correspondence in size and shape of this pair, that they have arisen from an elongated binucleate cell by the formation of a divisional cell wall. In one instance, I have found a cell wall *fully formed before division of the nucleus was completed* (Fig. 27). It cuts across the fine connecting thread at about the middle point of the latter. This must be considered as in some degree abnormal, especially since it was found in a serosa the nuclei of which had evidently degenerated.

Although division of the cell is almost always accomplished by the formation of a cell wall, I have found several *constricted cells*, showing that division may be partly, or even wholly, effected in this manner. Sometimes the constriction is so deep that the opposite walls meet (Fig. 28); but it is more usual to find that, after the cell has become considerably constricted, a cell wall is formed joining the inward curves of the constriction, and completing the division. At first, I thought it possible that the constriction was mechanically produced by the pressure of growing cells on either side. But this would not explain the invariable occurrence of the constriction at precisely the point where it would take place in a free cell, — equidistant from the daughter nuclei. Furthermore, the curvature of cell walls (see Fig. 13), which is almost certainly caused by the growth of cells and consequent tension, has no reference to the position of the nuclei.

As far as can be judged, the daughter nuclei are, as a rule, of equal size, and alike in shape. I have found many instances of beautifully symmetrical division (Figs. 9 and 10); but the nuclei of the serosa are not altogether exempt from the irregularities that seem to be inseparable from amitotic division wherever it occurs. Sometimes the resulting nuclei are obviously unequal (Fig. 13), even in young membranes; and in old membranes, where the nuclei have undergone degeneration, not only are the daughter nuclei extremely irregular in shape, but often very dissimilar in size.

Relations of the Nuclei to the Cell. — A very brief examination of a preparation of the serosa convinces one that the nuclei are symmetrically arranged in the cells. When there is but one nucleus, it occupies the centre of the cell; when there are two or three nuclei, each presides over a half or a third of the cytoplasm. This arrangement is so constant, that any marked deviation from it catches the eye at once. Instances of decidedly unsymmetrical arrangement of nuclei, one of which Figure 13 represents, are very unusual. As regards elongated cells, the daughter nuclei lie in the *long axis* of the cell, and at approximately equal distances from its ends. Occasionally, however, the nuclei lie in the *short axis* (Fig. 12), and much more frequently are placed *obliquely*, as in cell *a*, Figure 14. We would suppose that, in the event of division of an elongated cell with nuclei lying transversely, the cell wall would pass longitudinally between the nuclei; but I have not been able to find evidence of longitudinal divisions. From the large number of cells with nuclei lying obliquely, one would infer that oblique division of the cell often took place. I am unable to discover, however, that such is the case; and it seems extremely probable that the divisional plane of the cell does not always coincide with that of the nucleus.

I have found about 25 cells of the serosa with three nuclei. This seems to be a matter of individual variation in the make-up of the membrane, for all but three of the trinucleate cells were in membranes from the brood of a single scorpion, and membranes from some broods appear to have none. I have in one instance found a *group* of trinucleate cells (Fig. 14, *1*, *2*, *3*, *4*). At this spot nuclear multiplication has outstripped cell multiplication. It is nearly always easy to see which of the two original nuclei has divided, for we find two of the nuclei smaller than the third, and nearer to each other than to the latter. In cell *2*, for instance, the pair of nuclei on the left have arisen from a nucleus occupying a position about midway between them. The same statement would doubtless hold true for the two nuclei on the right in cell *3*, and here the odd nucleus is elongated. When the cell is long and the nuclei all lie in the longitudinal axis, as is the case in cell *1*, it is usually impossible to determine which of the two original nuclei has divided; for the nuclei are equidistant, and nearly alike in size. Another type of equidistant nuclei is shown in cell *4*, — a distribution quite as characteristic of very large, broad cells as the linear arrangement is of elongated cells. I have spoken of the division of one of the two original nuclei as though it always took place *after* the nuclei were completely separate, and had taken their positions in the cell. This seems to be the usual method, for I have several times found one of the original nuclei in the act of dividing. But it is possible, of course, for them to arise by a tripartite division, in which the three nuclei would be formed simultaneously. I have found only one instance of a true triple division, represented in Figures 29 and 30, and as this occurred in a serosa which had plainly undergone degeneration, I do not consider it as altogether normal. It will be noticed that the original nucleus became trilobed, and that the lobes became daughter nuclei of approximately equal size by the formation of three divisional planes, meeting at the centre of the original nucleus. The daughter nuclei on the right are still united to each other by strands at the corners. Very similar tripartite divisions were found by Overlach ('85, Plate XI. Figs. 35 and 41) in the epithelium of the cervix uteri. In two other cases, I have found one of the daughter nuclei in a late stage of division (Figs. 31, 32) *itself* elongating and undergoing constriction. It will be noticed that the constricted daughter nucleus is considerably larger than its mate.

I have found but two cells with more than three nuclei, and these both contained four. This condition is brought about by the division of both nuclei of a binucleate cell. On *a priori* grounds, one would reason that quadrinucleate cells would be nearly as abundant as those with three nuclei, for, apparently, it must often happen that a pair of daughter nuclei, arising as they do by a symmetrical and accurate constriction, are ready to divide at almost the same moment. Yet there are doubtless influences which operate to prevent the division of one of the nuclei. Although it is of course impossible to generalize on the characteristics of quadrinucleate cells, it may be of interest to mention the peculiarities of the two found. They are both large cells, of nearly equal width at the ends, and the breadth of both exceeds half the length. In one, both pairs of nuclei lie transversely, showing that the second divisional plane was at right angles to the first. In the other, represented in Figure 33, the lower pair of nuclei lie in the longitudinal axis, the upper pair almost transversely. One of the quadrinucleate cells is considerably larger than any cell near it, while the other (Fig. 33) though by no means small, is of much less dimensions than the immense bi- and uninucleate cells around it. I am unable to assign any reason for the multinuclear condition of this cell. One fact, however, is worthy of note. The united volume of its four nuclei does not exceed the bulk of the *single* nucleus of a neighboring cell. One cannot, of course, ascertain what the size of the primitive nucleus of the multinucleate cell was, but it is very improbable that it exceeded in volume the nucleus of the uninucleate cell in question, for the latter cell is considerably the larger of the two, and throughout this serosa the size of the nuclei bears a direct ratio to the size of the cells.

As regards the influence or influences impelling nuclei to divide independently of the division of the cell, nothing very definite can be stated. It is certain that the *absolute* or *relative size* of *the cell has little or no influence upon the division of the nucleus.* There are cells of all sizes, from the largest to the very smallest (Fig. 3), which are binucleate; and it is usual to find, side by side with bi- or multinucleate cells, others with a single nucleus that are actually larger than the former (compare the cells in Figure 14). In such cases, the single nucleus is always larger than the daughter nucleus of the other cells. I am unable to see that multiplication of nuclei in the cell leads to any immediate increase of nuclear material. The more they divide, the smaller they become. Probably the most important office of division is *a more extensive distribution of nuclei throughout the cytoplasm, with corresponding increase of nuclear surface;* and this, considering the great superficial extent of the cells, and the comparatively small size of the nuclei (at least in the older membranes) must be a matter of some importance for the activities of the cell. It is especially so in the case of *elongated* cells. If such cells have but a single nucleus, a large part of the cytoplasm must be remote from it; and if the nucleus is at the centre of the cell, the cytoplasm at the ends of the cell will be most remote. So, to restore the equilibrium between cytoplasm and nuclei, the nucleus must elongate in the longitudinal axis of the cell, and the daughter nuclei move toward the ends of the cell.

As a matter of fact, nearly all elongated cells have two nuclei, and these lie in the long axis of the cell, usually rather nearer its ends than to each other. It cannot be denied that many short or squarish cells also contain two nuclei; and, conversely, a few much elongated cells can be found that have but one. In the latter case, it is interesting to observe that almost invariably the nucleus has begun to elongate in the longitudinal axis of the cell, and is often far advanced towards division. We can say almost with certainty, then, that such cells are of recent formation, and that the equilibrium between cytoplasm and nucleus is promptly restored by division of the latter. It is true that cases like that represented in Figure 12, where nuclear division takes place in the short axis of an elongated cell, cannot be explained in this manner. Such instances are so rare that they might almost be considered as abnormal; but the difficulty of the matter lies in the fact that we get *all gradations* between nuclei ranged in the true longitudinal axis, and those placed in the transverse axis. It is common to find them lying more or less obliquely in the cell, though the obliquity is seldom so great as to prevent them from practically fulfilling the conditions of the hypothesis.

It is not supposable that all the agencies impelling nuclei to divide, and controlling the direction in which division shall take place, reside in the cytoplasm; possibly the most potent of them exist in the nucleus itself. That axial differentiation, with definite pole and antipole, is as characteristic of the resting nucleus as of the mitotic nucleus, was postulated by Rabl ('85, p. 323) from a careful study of the chromatic network in the "skein stage" of mitosis. In a recent paper ('89, pp. 23, 24), the same writer states that the "polar depression," usually visible in young daughter nuclei, persists much longer than usual in the epithelial nuclei of the Triton; so that for these mitotically dividing nuclei it is highly probable that polar differentiation is *always* present in the resting state. Carnoy ('85) has shown that, in the resting nuclei of the testicular cells of certain Arachnids, the chromatic filaments are distinctly arranged with reference to a definite axis (Planche V. Figs. 165–169), and Van Gehuchten ('89) has found the same in glandular cells of a Dipterous insect, *Ptycoptera contaminata*.

It is obvious that the discovery of an "organic axis," as Van Gehuchten calls it, in amitotically dividing nuclei is more difficult, for here there is no polar depression or longitudinal arrangement of chromatic filaments to indicate its direction in the resting nucleus. It is usual for each division of the nuclei of the serosa to take place at right angles, or nearly so, to the plane of the previous division. This is well seen in many multinuclear cells, where one or both pairs of nuclei lie transversely in the cell, and therefore at right angles, or nearly so, to the direction of the first division (see cells *2* and *3*, Fig. 14). In other cases, however, two consecutive divisions take place in the same direction (Fig. 14, cell *1*). It occurred to me that possibly there was an organic axis in the nuclei of the serosa which in some cases exerted a controlling influence upon the direction in which division took place, but which in most instances was counteracted by influences resident in the cytoplasm. Transverse divisions of the nucleus (Fig. 12) could then be accounted for by assuming that the influence of the organic axis is dominant in these cases, while oblique divisions would be explainable on the ground that neither influence was predominant, but that *both* acted with about equal force in directions at right angles to each other. A question of interest in this connection is, whether, when the cytoplasmic influence is dominant, and tends to make the nucleus divide in a plane parallel to its organic axis, division actually does take place in that direction. If such were the case, an organic axis would be a fact of slight morphological importance, and the longitudinal arrangement of chromatin, which takes place in the earlier stages of constriction (Figs. 4, 6, 7), might occur in any direction, without reference to an organic axis. If, on the contrary, it were necessary that the longitudinal filaments should be arranged *parallel* to the organic axis, in order that division might take place *transversely* to the axis, this result could still be attained by a *rotation of the nucleus*, even when the tendency was for the nucleus to divide at right angles to the previous division. It is obvious that rotation would occasionally be apparent, provided it took place soon after division, and *previous* to the absorption of the proximal end of the connecting filament. I examined a large number of preparations to find evidence of rotation, but I must admit that the evidence was slight, and hardly sufficient to establish the hypothesis which I had formulated. It is therefore put forth provisionally, in the hope that it may lead to further investigations in this line.

The most striking instance of rotation was found in one of the quadrinucleate cells (Fig. 33, nuclei *a* and *b*). It is evident that three nuclear divisions have taken place without any division of the cell, producing two, three, and four nuclei. The arrangement of nuclei makes it reasonably certain that the *lower* pair arose by division of one, and the *upper* pair by division of the other nucleus of the binuclear stage. Only under this supposition could the daughter nuclei of that stage have had the normal arrangement, to which all the neighboring cells rigidly conform. We further find, that, while the upper pair of nuclei has arisen by a division in the long axis of the cell, the lower pair has been produced by division in the transverse axis, and therefore in conformity with the law previously stated (p. 136). One nucleus of each pair (*a* and *b*) retains a remnant of the connecting filament, which is directed, not toward the sister nucleus, but to a point 90° distant from it. This condition could have been brought about only by rotation of the nuclei, which in both cases has been through an arc of 90°.

In the serosæ from older embryos, the daughter nuclei almost invariably recede from each other in the course of division. The amount of recession is governed by the length of the cell (Fig. 15). In the younger membranes, as already stated, the constriction is deep and narrow, so that the nuclei not infrequently lie very near together (Fig. 13). In these young membranes, however, the nuclei are larger, and the cells are usually smaller, than in the old membranes. Since, moreover, the *large* binucleate cells of young membranes almost always have their nuclei symmetrically placed at the ends, it is probable that the nuclei gradually move apart *after* division, as the cell increases in size.

It will be seen that my interpretation of the primary cause of the division of these nuclei agrees in part with the hypothesis advanced by Chun ('90) for the explanation of amitotic division in general. This is, in brief, that the object of amitotic division is the distribution of nuclear material throughout the cytoplasm, with corresponding increase of nuclear surface. He considers it the final phase of a series of conditions which begins with a simple lobed nucleus, and includes branched nuclei of various degrees of complication. In support of this interpretation, Chun lays stress on the statement that cell division, after an amitotic division of the nucleus, has seldom or never been observed with certainty, thereby implying that amitosis cannot have in view the multiplication of cells. I do not consider this as essential to the hypothesis, nor, in fact, do I believe him correct on this point. The evidence of cell division after amitosis seems to me abundant and conclusive. It was observed by F. E. Schulze ('75) in *Amœba polypodia;* by Ranvier ('75), Bütschli ('76), Flemming ('82), Arnold ('87), and others, in leucocytes; by Kükenthal ('85), in the lymphoid cells of Annelids; and by Carnoy ('85), in various cells of Arthropods. As the foregoing shows, there is abundant evidence that, in the serosa of the scorpion, division of the cell *sometimes*, at least, follows amitotic division of the nucleus. Furthermore, the extremely regular and well ordered manner in which the nuclei divide, and the similarity as to size and shape of the daughter nuclei, seem to me decidedly against the notion that the *sole* object of the division is to disseminate nuclear substance in the cytoplasm; for in those cases where amitosis is not followed by division of the cell, and assumably takes place simply for the purpose of dissemination, the nuclear products are very variable as to number, size, and shape.

II. The Amnion.

Plate I. Figs. 1 and 2; Plate II. Figs. 16-20.

The amnion is much thinner than the serosa, and like it is composed of a single layer of flat, polygonal cells (Fig. 1, *am.*). But, while both the cells and nuclei of the serosa have become enormously larger than the blastodermic cells from which they originated, those of the amnion have changed little as regards size. The boundaries of the amniotic cells are not always visible, and I find that preparations, even when hardened and stained in the same manner, show the greatest variation in this respect. As a rule, the cell walls in the amnion are sharply and clearly defined *only* in preparations of membranes from advanced embryos. The same is true of the cell walls of the serosa.

In general, the amniotic cell has but one nucleus, which usually occupies the centre of the cell. Blochmann makes the same statement as to the number of nuclei in each cell, and he found no evidence of division among them. The outline of the nuclei, which measure about 15 μ in diameter, is frequently somewhat irregular or lobed. Like the nuclei of the serosa, they are flattened tangentially (Fig. 2, *nl. am.*); but notwithstanding this, they cause an outward bulging of the cell upon the serosa, as shown in Figure 2. They contain always one or more highly refractive, deeply staining nucleoli. The rest of the scanty chromatic substance is in the form of minute granules, occasionally arranged partly in a very faint network (Fig. 18, *b* and *c*). As in the nuclei of the serosa, chromatic threads frequently unite the nucleoli.

Division of the amniotic nuclei is of rare occurrence. In only one of my preparations are dividing nuclei at all abundant. The division takes place without mitosis, but is of a different type from that of the nuclei of the serosa. The only alteration of the chromatin is possibly a change in the position of the nucleoli; I have not been able to detect any modification of the reticulum. The first sign of approaching division is elongation of the nucleus (Figs. 16 and 18, *a*). A deep narrow constriction appears at the equator of the nucleus (Fig. 17). This is followed by the formation of an equatorial septum, at once partitioning off the nucleus into two daughter nuclei (Fig. 18, *b*). If there are but two nucleoli, it is the rule to find one in each daughter nucleus; but where there are several, they are often unequally apportioned. After the formation of the septum, the daughter nuclei still adhere to each other, and division seems always to be attained by deepening of the equatorial constriction in the plane of the septum (Figs. 18, *b*, *c*, and 19). I have not found any evidence of a recession of the nuclei before division of the cell. Furthermore, the rarity of binucleate cells makes it very probable that cell division follows nuclear division promptly. As in the serosa, division of the cell takes place by the formation of a cell wall without marked constriction (Fig 20). The position of the nuclei in this figure, and the frequency with which nuclei are found near the boundaries of the cells (Fig. 1, *am.*) is evidence of the promptness of cell division after the division of the nucleus.

It is clear that Chun's hypothesis will not hold in this case, for there is even less tendency than in the serosa to accumulate nuclei in the cell. This may be owing in part to the *shape* of the cell, for it is seldom elongated. It would seem that, in case the cell becomes elongated, nuclear division takes place and the cell divides immediately after the nucleus. The orientation of the nuclei with reference to the cytoplasm of their respective cells would then be accomplished by their migration to the centre of the cells.

III. The Ovarian Capsule.

Plate II. Figs. 21-26.

The epithelium of the ovarian capsule is not often easily made out in ordinary stained preparations, for the nuclei of muscle fibres and connective-tissue cells lie not only just external to the epithelial nuclei, but frequently in the same plane with them. In most of my preparations the boundaries of the epithelial cells cannot be seen at all, and I have therefore confined my attention mainly to those which show them distinctly. In shape, the cells are more or less irregular, oblong hexagons (Figures 24 and 25 represent typical shapes). The cell walls are broad and fibrillated, like those of the serosa, though the cells themselves are smaller even than those of the amnion. The nuclei are not only larger in proportion to the cells, but often larger absolutely, than the amniotic nuclei. The amount and arrangement of the chromatin in the capsular nuclei (except in a certain phase) is almost precisely like that already described for the nuclei of the amnion, but there is usually only one conspicuous nucleolus. The small amount of chromatic substance, aside from the nucleolus, has a granular appearance, but sometimes shows indications of a filamentous or reticular arrangement (see Figs. 21, 23, 24). Seen in face view, the nuclei are circular, and have a distinct nuclear membrane. The section (Fig. 2, *nl. fol.*) shows that they are less flattened than the amniotic nuclei.

Here, again, we have amitotic division, and of precisely the same type as prevails in the amnion. Apparently, division is not of common occurrence, for I have been able to find only a few instances, and have, unfortunately, not seen its earliest stages. Figures 21, 22, and 23 show the simple manner in which it is effected. As each daughter nucleus contains a nucleolus, and the ordinary resting nucleus has but one, division of the nucleolus must precede division of the nucleus. In one important respect the division of these nuclei differs from that of the amniotic nuclei. The cell does not divide immediately after the nucleus, and consequently a great number of cells are binucleate. Some even contain three nuclei. I have obtained no evidence whatever of cell division.

IV. Degenerative Changes.

Plate II. Figs. 14, 24-26; Plate III. Figs. 28, 34.

The striking difference in the appearance of cells and nuclei, and the different manner of division of the nuclei, exhibited by serosæ of different ages, have frequently been referred to. Such changes, in part at least, I believe to be due to degeneration of the membranes, which, with the exception of the ovarian capsule, are temporary structures, soon to be cast off by the embryo. Hence it is not surprising to find them undergoing degeneration *in toto*. The degenerative changes are about equally well marked in all three membranes; but on account of the great size of cells and nuclei, the changes are most conspicuous in the serosa. If the membrane comes from a young embryo, the walls of the cells are unstainable, and therefore often difficult to make out. The nuclei have a vesicular appearance, with smooth, rounded contour, abundant karyoplasm, and scanty chromatic substance. For this reason the nuclei seldom stand out clearly from the cytoplasm in a stained preparation, often being no darker than the rest of the cell.

Serosæ from somewhat older embryos, while giving no sure signs of degeneration, have nuclei slightly different from those of the youngest membranes. The amount of chromatic substance appears to be larger. It is gathered into denser and more deeply staining masses, and the nucleoli become larger and more stainable (compare Figures 4 and 5, the former from an older membrane than the latter). Many nuclei at this stage become irregular in outline, and are more or less shrunken in appearance, changes which prepare the way for complete degeneration, found in membranes from the oldest embryos. The nucleus here becomes shrunken into a formless mass, which stains deeply and uniformly. This condition seems to be due almost wholly to loss of the karyoplasm, for the nuclear membrane is seen to be drawn closely over the much condensed chromatic substance. The uniformly staining effect, however, is generally believed to be produced by the solution of a part of the chromatin in the karyoplasm; this is best seen in nuclei that have not completely degenerated, where the deeply stainable solid chromatin is immersed in the less stainable matrix. Not all the nuclei in a membrane are affected to the same degree by the degenerative change. This is shown in Figure 14, where the nuclei of cell *a*, and that of the cell farthest to the left, are more affected than any others. But in the oldest membranes almost every nucleus has undergone extreme degeneration.

It is an interesting fact, that even the most thoroughly degenerated membranes have numerous nuclei in all stages of division. The dividing nuclei have undergone the same degenerative alteration as the rest. It is impossible to state whether these nuclei had begun to divide *after* the regressive change, or had been overtaken by these changes while undergoing division; and it is equally impossible to say whether degeneration would have prevented the nuclei from completing their division. The division is essentially like that of younger nuclei, but often unsymmetrical.

Not all the degenerative changes are confined to the nuclei. The cells also give evidence of modification. Their walls become more distinct, not only because they are denser and thicker, but on account of their stainability with hæmatoxylin. The cytoplasm frequently has a reticulated structure, which is densest about the nucleus. In the oldest membranes, certain large groups of cells have nuclei surrounded by a narrow bright ring, and outside this a much broader halo of a radiating structure, which takes a deeper stain than the rest of the cytoplasm (see Fig. 34). The appearance of the whole is strikingly like that of the "attraction spheres" of ovarian and other cells, but in this case has certainly nothing to do with mitosis. If the cell contains two nuclei, or a dividing nucleus, each daughter nucleus is surrounded by a halo. In early stages of division, however, the elongated nucleus has a single halo. I am unable to account for these appearances; I do not regard them as attraction spheres, but rather as a result of degeneration. The attraction sphere should radiate from a centrosome; here it radiates from the nucleus as a centre. I may state, in passing, that my search for centrosomes in the serosa has been wholly unsuccessful. The pale ring is very generally present around nuclei that have undergone degeneration. It seems to have no intimate connection with the radiating zone, being frequently found where the latter is absent.

The life history of the serosa cells corresponds closely with that of certain cells in the Malpighian vessels of *Aphrophora spumaria* described by Carnoy ('85, p. 219). The cells at the two extremities of the tubes contain nuclei not greatly different from those of young serosæ, but the nuclei of the middle portion are irregular, jagged, and filled with amorphous chromatin. They therefore bear a strong resemblance to the degenerated nuclei of the serosa. Furthermore, the origin of the peculiar nuclei of the middle portion of the Malpighian vessel agrees closely with that of the degenerated nuclei of an old serosa. It is thus described by Carnoy (p. 220): "Sur les petites

larves on rencontre tous les intermédiaires entre les noyaux des extrémités et ceux du milieu. Peu à peu le boyau s'efface, le noyau lui-même se rétrécit et perd la régularité de ses contours à cause du plissement de sa membrane ; à la fin la nucléine ne forme plus à l'intérieur qu'une masse compacte et homogène, à peu près comme cela se présente dans la tête des spermatozoïdes." In both cases the degenerated nuclei are found in stages of division ; in both, the cytoplasmic reticulum is distinct only in old cells, and where these cells are binucleate it is dicentric, with filaments radiating from the nuclei. The *dicentricity* of the binucleate cells is a point to which Carnoy calls special attention (p. 229). He considers that here the radiating filaments of the cytoplasmic reticulum answer to the polar asters of karyokinesis, and that the nucleus has the function of a centrosome. The same reasoning would apply to the degenerated cells of the scorpion's serosa.

The regressive metamorphosis undergone by the epithelial cells of the ovarian capsule (Figs. 24–26) is very peculiar. Here, again, the cell walls are affected in the same way as in the serosa and amnion, for they are not distinctly seen until after the nuclei have degenerated. Nearly all of the epithelial cells of an old capsule have two nuclei, which are dissimilar in size and appearance (Figs. 24 and 25). The smaller takes a rather deep, uniform stain, almost as dark as that of the chromatin of the other. A nucleolus is always present, and frequently minute granules of chromatic substance. The uniformly staining character of the nucleus is doubtless produced by chromatic substance held in solution by the karyoplasm, a condition of common occurrence with degenerating nuclei. The larger nucleus (Figs. 24 and 25) takes only a slight stain, owing to the scantiness of its chromatic substance, which is present in the usual form of isolated granules and an imperfect network. By examination of a large number of cells, I found nuclear differentiation of every degree, beginning with nuclei almost alike in size and stainability (Fig. 24), then passing to examples of marked dissimilarity (Fig. 25), where the pale nucleus has become almost invisible, and the smaller deeply staining one has attained a very sharp, definite outline. As the pale nucleus becomes more and more shadowy, its shape becomes irregular. Near cells of this sort others can be found which contain only a single deeply staining nucleus (Fig. 26), the other having disappeared altogether. In case of trinucleate cells, I have invariably found two of them to be of the pale sort.

I am unable to offer any other explanation of these changes than that they are the result of degeneration or of decreased activity of the tissue.

But why one nucleus should become altered in one way, and the other in an entirely different manner, is difficult to say. A very similar differentiation of nuclei has been observed by Chun ('90) in the egg germs of a Siphonophore (*Stephanophys*). He found only *one* nucleus in the youngest germs, while the middle-sized and larger egg cells contained *two* of different size, the larger being pale, and the smaller staining intensely. The smaller nucleus moves to the periphery of the egg and is no longer visible when the latter is ripe. The larger nucleus persists as the germinative vesicle. In only one instance did he see a stage that showed that the smaller nucleus *budded out* of the larger. Chun compares the small, deeply staining nucleus to the "Stoffwechselkern" (macronucleus), and the pale one to the "Fortpflanzungskern" (micronucleus) of the ciliate Infusoria.

Summary.

1. The embryo of the scorpion is enveloped by three membranes, the ovarian capsule, the serosa, and the amnion.

2. The ovarian capsule is an enlargement of the ovarian tube; the serosa and amnion arise from the blastoderm of the egg.

3. Serosa and amnion are at first distinct, and joined to each other by minute fibres. These afterwards disappear, and the membranes coalesce.

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4. The serosa is composed of immense flat cells, very variable in size and shape. The cell walls are fibrillated.

5. The majority of the serosa cells have two large nuclei of equal size. There are rarely more than two.

6. The nuclei are disk-shaped, have a distinct nuclear membrane, and chromatin in the form of granules and filaments, the latter forming an indistinct reticulum. There are usually several nucleoli.

7. The cytoplasm of the serosa has a distinct reticular structure.

8. Nuclear division in the serosa is amitotic, and takes place by constriction, preceded by elongation of the nucleus. It is followed or accompanied by recession of the daughter nuclei, which remain for some time connected by a fine strand.

9. Constriction of the nucleus is usually accompanied by a longitudinal arrangement of some of the chromatic threads, radiating from the constricted part. The nucleoli are distributed about equally to the daughter nuclei.

10. Nuclear division may be followed by division of the cell, but not often immediately. The cell divides by the formation of a cell wall, either with or without constriction.

11. The binucleate condition of cells is independent of their size; but, in general, the size of the nucleus, or nuclei, is proportional to the size of the cell.

12. Elongated cells of the serosa are generally binucleate. The nuclei almost invariably lie in the long axis of the cell, near the ends.

13. A binucleate cell becomes trinucleate by division of *one* of its nuclei, and quadrinucleate by the division of *both*. Very rarely the division is tripartite, and the three nuclei are produced simultaneously from a single one.

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14. Division of the amniotic nuclei is also amitotic, but the constriction is supplemented by a septum at the equator of the elongated nucleus.

15. There is apparently no rearrangement of the chromatic substance. Nucleoli are apportioned equally to the daughter nuclei.

16. Division of the nucleus is quickly followed by division of the cell, so that binucleate cells are not common.

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17. The epithelium of the ovarian capsule is composed of small hexagonal or rectangular cells, which frequently contain two or more nuclei.

18. The nuclei are very similar to those of the amnion, but usually contain only one nucleolus.

19. Nuclear division is amitotic, and precisely like that of the amniotic nuclei. Each daughter nucleus contains one nucleolus.

20. No instance of cell division was observed.

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21. All three membranes undergo degeneration as the embryos approach maturity.

22. In the serosa the cytoplasmic reticulum becomes more distinct, and is seen to radiate from the nuclei. The cell-walls become stainable.

23. The chromatic substance of the nuclei becomes grouped into dense masses; the reticulum and nucleoli become more distinct. The outlines of the nuclei become irregular.

24. As degeneration proceeds, the cytoplasm frequently forms a halo of radial structure around the nucleus.

25. The nuclei finally become reduced to uniformly staining, irregular masses of chromatin, which has partly entered into solution. Such nuclei are found in all stages of division.

26. In binucleate cells of the ovarian epithelium the nuclei become dimorphic.

27. The chromatic substance of one of the nuclei enters into solution in the karyoplasm, and the nucleus becomes reduced in size.

28. The other nucleus loses its stainability, and increases in size. It finally disappears.

V. Discussion of Amitosis.

As long as karyokinesis was supposed to be a uniform process, all the complicated details of which were carried out with the greatest exactness and in the same sequence, wherever it occurred, no one sought to homologize it with the little known and far simpler "direct" division. The latter had, apparently, so restricted a range, and had received so little attention, that its very existence was denied; and it was generally anticipated that, in the few kinds of cells in which it was stated to occur, a better technique and more careful study would reveal mitotic phenomena. This opinion seemed to receive confirmation by the discovery of mitotic division in leucocytes and the Protozoa, thus carrying mitosis back to the simplest types of cells and to the lowest forms of life. The ascertainment of two facts has brought about a radical change in our views regarding amitosis: (1) the variability of karyokinesis, including, in some cases, the omission of apparently essential steps; and (2) the wide occurrence of amitosis, new instances of which are constantly coming to light in various parts of the Animal Kingdom. Inasmuch as it became necessary to recognize the existence of direct division, efforts were naturally made to find links connecting it with mitosis; the variability of both mitosis and amitosis seemed to lend strength to the theory which refers them to a single fundamental plan of division. In this scheme, amitosis is considered either as a primitive method from which mitosis was evolved, or else is looked upon as a degenerate form of mitosis, occurring in nuclei which, from their pathologic or exhausted condition, have lost the power of dividing by the more complicated process. By fixing epithelium of the salamander larva with osmic acid, then treating it with Müller's fluid, and finally staining with hæmatoxylin, Pfitzner ('86^a) has shown conclusively that, even in cases of very perfect mitosis, the karyoplasm maintains its integrity, and divides by a simple constriction, as in direct nuclear division. This fact has led Waldeyer ('88) to the conclusion that karyokinesis in based upon the simple scheme of division conceived by Remak. He says: "I would interpret the facts in such a way that we have to regard as the fundamental form the simple amitotic division, which is now proved for many cases; it always takes place where the nucleus either is poor in chromatin, or when it does not matter about strict bipartition of the chromatic material. Should the latter be required, then we shall find mitosis, since it is the most direct, most certain, and most simple manner in which an exact bipartition of chromatic substance is brought about."

It seems to me, however, that there are differences of so fundamental a character between mitosis and amitosis, as at present understood, that it is impossible to refer them to a single plan of division. Both, indeed, achieve the same result, — division of the nucleus, including its two constituents, chromatin and karyoplasm. In both cases, the karyoplasm divides by constriction. In amitosis, the chromatin undergoes little if any change in preparation for division; in mitosis it becomes consolidated into a limited number of thickened rods or loops (chromosomes), which arrange themselves in the plane of division ("mother star," "couronne équatoriale") and segment either longitudinally or transversely, the halves moving to opposite poles ("diaster"), and undergoing a reversed metamorphosis to form two daughter nuclei. If this were all there is to karyokinesis, — and in some cases the process is much simpler, — we might hope to find transitions between it and amitosis; for there are examples of amitosis in which the chromatic network undergoes changes during division, and it would be conceivable that the highly organized changes of the chromatic substance during mitosis were either evolved from them, or that they were a simplification of the more detailed changes. In mitosis, however, other structures besides chromosomes make their appearance, — the *centrosomes*, *attraction spheres*, and *spindle*. These structures are not known to take any part whatever in amitosis, and in this respect at least the two kinds of division are fundamentally different. The most recent workers upon karyokinesis agree in assigning to the spindle rays the function of *separating or dividing the chromosomes, and drawing (or pushing) the segments towards the poles.* The centrosomes are focal points towards which the spindle rays converge, and lie *entirely outside the nucleus.* The formation of the spindle has been carefully studied by many investigators of karyokinesis, and, while there are very divergent views as to its origin and mode of action, the most recent workers in this field (of whom

E. van Beneden, Boveri, and Watase may be mentioned) are agreed that the spindle arises *from the cytoplasm.* The same view with regard to the spindle in the mitosis of vegetable cells was expressed by Strasburger, Guignard, and other botanists.

The centrosome, as a converging point for the spindle fibres and polar rays, plays a most important part in karyokinesis, and, so far as known, none at all in amitosis. The centrosome has indeed been found by Flemming ('91) in leucocytes, which certainly divide amitotically; but there it is a single structure, and as Flemming's figures show, *takes no part in the amitotic division of the nucleus.* Whether it also remains passive during the *mitotic* division of leucocytes and in amitosis followed by division of the cell, is not known. It has been supposed by Carnoy ('85) that spindle rays were present in certain nuclei which divide amitotically, but this seems extremely doubtful, especially since they have no perceptible action on the chromatic substance. I believe it can be shown in every case of amitosis known, that the division of the chromatin is accomplished *independently of chromosomes, spindle rays, or any other visible influence outside of the nucleus.*

The persistence of the nuclear membrane in amitosis, and its disappearance in mitosis, were formerly considered points of distinction between the two kinds of division; but, as is well known, more recent studies have shown that the membrane persists in many cases of undoubted karyokinesis, especially among the Arthropods (Carnoy, '85) and Protozoa (Gruber, '83, R. Hertwig, '84, Pfitzner, '86^b, and Schewiakoff, '88). Its presence seems to offer no obstacle to the karyokinetic changes, and Watase ('91) has pointed out that it need not prevent the formation of an extra-nuclear spindle, the rays of which may penetrate the membrane. In the nuclei of *Opalina ranarum*, and in the micronuclei of Infusoria generally, where, according to all observers, the nuclear membrane persists, the mitotic division is accompanied by constriction; but the fact that constriction is here *visible* may be considered as in some measure a *result* of the persistence of the membrane, thereby making evident the outline of the karyoplasm. Yet constriction does not always take place when the membrane persists, for in the spermatic cells of *Pagurus striatus*, figured by Carnoy ('85, Plate VII. Fig. 244), the nuclear membrane is visible at all stages, and gives no evidence of constriction.

The modification of the chromatic substance into chromosomes is usually the most conspicuous feature of karyokinesis, and in most cases serves to distinguish mitotic nuclei from any of the amitotic ones. The chromosomes invariably include *all* the stainable substance of the nucleus, so that the presence of nucleoli in a nucleus undergoing constriction may be taken as perhaps the strongest evidence of direct division. The behavior of nucleoli in amitosis is of peculiar interest. Where there is a single nucleolus, it constricts previous to the constriction of the nucleus, according thus with the Remakian scheme. The division of the nucleolus, however, has rarely been observed. It was first described, I believe, by F. E. Schulze ('75), in the division of *Amœba polypodia;* has since been figured by Carnoy ('85, Plate I. Figs. 10, 12, 13) for various amitotically dividing Arthropod cells, and by Hoyer ('90) for the intestinal epithelium of *Rhabdonema nigrovenosum.* A peculiar modification of the nucleolus, and its division into four segments previous to the constriction of the nucleus, was observed by Platner ('89, pp. 145–149) in the Malpighian vessels of *Dytiscus marginalis.* It is extremely probable that, whenever the nucleolus is a single and definitely organized structure, it always divides previously to or during constriction of the nucleus. Where there are several small nucleoli, they may indeed arrange themselves so as to be equally apportioned to the daughter nuclei; but they are not known to divide, as the chromosomes in mitosis do.

Amitotic division, even more than karyokinesis, is variable in its phenomena. It takes place by constriction, by formation of division planes, by gemmation, and by enlargement of one or more perforations (Arnold, '88, Flemming, '89). It is either simple or multiple, and it may or may not be accompanied by division of the cell. The resulting nuclei may be equal or unequal. Amitosis occurs throughout both the Animal and Vegetable Kingdoms; but as far as animals are concerned, it is far the most frequent among *unicellular organisms, amœboid cells (leucocytes), and epithelial tissues.* There seem to be no authentic instances of it in connective tissues (except possibly the fat-cells of Arthropods, described by Carnoy), none in nervous tissue, and but one or two in muscle fibres (Carnoy, '85, p. 221). Not only the nuclei of fixed tissues divide by the direct method, but also those of nascent tissues, at least among the Arthropods. Direct division is, however, of rare occurrence in the embryo. I believe there are only two authentic instances of it, — that discovered by Carnoy in the ventral plate of an embryo of *Hydrophilus piceus* ('85, p. 224, Plate I. Fig. 11), and that found by Wheeler ('89, p. 313) in the formation of the blastoderm of *Blatta germanica,* where no instance of mitosis was detected. The embryonal membranes of the scorpion I do not include under this head, because they are temporary structures forming no vital part of the embryo.

Among the Metazoa, epithelial tissues offer by far the greatest number and the most interesting cases of amitosis. Furthermore, as Ziegler ('91) has very recently shown, *epithelial cells of unusual size, with some peculiar functional activity (generally secretion) are most apt to exhibit this method of division.* Cell division has seldom been observed to follow amitosis in such large cells, which therefore become multinucleate. Other epithelial cells which frequently furnish instances of amitosis are those *which are near the end of their functional activity.* Cells of the *outer* layer of a stratified epithelium sometimes divide amitotically, while those of the *deeper* (and therefore *younger*) layers of the same epithelium divide by mitosis. A good instance of this was recently described by Dogiel ('90) in the epithelium of the bladder of Mammals. The nuclei of the large epithelial cells lining the intestine of Arthropods very commonly divide by amitosis, as was found by Frenzel ('85) in the midgut of *Astacus* and *Maja;* by Carnoy ('85) in the intestinal epithelium of Isopods; and by Faussek ('87) in the digestive tract of a Cricket (*Eremobia muricata*) and in the larva of *Æschna.* The intestinal epithelium in all Arthropods has an important secretory function. Cells whose function is excretory likewise exhibit amitotic division of the nucleus, as in the Malpighian vessels of Insects. The occurrence of amitosis in glandular and excretory epithelium is readily explainable on Chun's hypothesis, for the functional activities of such cells are peculiarly intense, and it is easy to see that a distribution of nuclear material in the cytoplasm is of advantage to the cell. The occurrence of nuclei of unusual size (as compared with the nuclei of other cells of the same animal) seems to me likewise referable to the peculiar needs of the cytoplasm in these cells.

Cases of amitosis peculiarly difficult of explanation are those presented by the germinal epithelium of the testis. So many observers have reported direct division in sperm mother-cells, that there seems no reasonable doubt of its occurrence. It has been suggested that the cells which divide amitotically never produce spermatozoa, but merely serve to secrete a fluid. This explanation, however, will not serve in the case of certain Isopods (*Oniscus asellus* and *Idotea* sp.) in the testes of which Carnoy ('85, p. 222) found amitosis the prevailing type of division, and mitosis of very rare occurrence. Direct division is found more or less frequently in the testicular cells of many other Crustacea, as the extensive work of Gilson ('84–87), and the investigations of Sabatier ('85) show, and occasionally in the other groups of the Arthropods. Among Vermes, it was found by Lee ('87) in Nemertians, and by Löwenthal ('89) in a Nematode (*Oxyuris ambigua*). It need hardly be said that amitosis in sexual cells is unexplained by any hypothesis yet offered regarding the biological significance of this type of division, and further investigations on this point are absolutely necessary before we can form any general opinion in regard to it.

In the maturation and segmentation of the ovum no instance of direct division is known, and it is here that karyokinesis is exhibited in its most complete form. The well known observations of Boveri ('87) on the segmentation of the egg of *Ascaris megalocephala* are of special interest on this point. He found a modification of the chromatic threads as early as the two-blastomere stage, one of them (cell A) retaining the four chromosomes characteristic of the nucleus after fertilization, the other (cell B) undergoing a reduction of its chromosomes into the form of granules. The two blastomeres arising by division of cell A undergo the same differentiation, the nucleus of one (cell A^1) retaining the chromatic loops, the other (cell A^2) undergoing reduction, so that in the four-cell stage only one nucleus has retained its chromatic loops. The systematic reduction of chromosomes was observed up to the 64-cell stage. The important deduction Boveri makes from these facts is, that the cells retaining their ancestral nuclear characters are the *Anlage* of the sexual cells of the developing animal, and that the cells whose nuclei undergo a modification of the chromosomes are all somatic cells. In accordance with this hypothesis, the division of both male and female sexual cells ought always to be karyokinetic, and of a somewhat different type from the karyokinesis of the somatic cells of the same animal. The latter statement, indeed, holds true for the testicular cells of the salamander, as was discovered by Flemming ('87). It also appears from the work of Carnoy, that in the post-embryonic life of Arthropods mitotic division is of rare occurrence in the tissue cells, but is of constant occurrence in the reproductive cells of the same forms.

As has already been stated (p. 147), attempts have been made to find a morphological connection between karyokinesis and direct division, and thus to solve the puzzling question of the relations they bear to each other. Carnoy ('85, p. 398) believes he has found transitions between them in the division of the numerous nuclei of *Opalina ranarum*. Some of these show a distinct spindle, others none ; in both cases the nuclear membrane persists, and division is accomplished by constriction. Pfitzner ('86^b), however, found only mitosis in *O. ranarum*. Carnoy has also seen transitional forms of division in the spermatic cells of

Pagurus striatus, and *P. callidus* (Planche VII. Figs. 244, 245). A nuclear plate is here formed, both in perfect mitosis and in degenerated mitosis; but in the former instance a spindle is formed, and the chromosomes segment individually, while in the latter the plate divides *in toto* by constriction, without the help of a spindle. This modified type of mitosis, if we may so regard it, Carnoy considered as the result of degradation (pp. 316, 317), inasmuch as it appeared only in *old* sperm mother-cells after spermatozoa had become numerous in the testis. This accords with the earlier view that direct division is concomitant with senescence of the nuclei, based especially upon nuclear division in plants (Schmitz, '79, Johow, '81). I have regarded this as a possible explanation of the occurrence of amitotic division in the embryonal envelopes of the scorpion, for these tissues are temporary structures which obviously are near the end of their functional activity. This explanation, however, will not fit all cases; for instance, the occurrence of amitosis in embryonic cells, and its prevalence in the testicular cells of some Isopods, already mentioned.

The hypothesis advanced by Chun seems to throw light upon many of the cases of amitotic division which are referable to a sort of *budding* or *branching* of the nucleus, carried to such a point that the buds or branches become constricted off as separate nuclear elements. These cases are, of course, not to be confounded with a disintegration of the nucleus, such as takes place in the macronucleus of Infusoria after conjugation, and sometimes in the degeneration of tissues. The distribution or extension of nuclear substance in the cytoplasm, whereby the surface of the nucleus is increased, is an event of frequent occurrence. It is seen in the many forms of lobed nuclei, such as those of the ovarian capsules of Amphibia (see Flemming, '82), and in those of leucocytes; in hollow or perforated nuclei (giant cells); in branched nuclei (spinning glands and Malpighian vessels of Lepidoptera); and in the band-shaped and moniliform nuclei of many Infusoria. These peculiar shapes are evidently produced by the *activity of the nucleus itself*, probably correlated with a special function of the cytoplasm. From the deeply incised lobation or band-shape of such nuclei it is an easy step to the formation of separate smaller nuclei by the deepening of a constriction already formed. Such daughter nuclei will as a rule be irregular in shape and unequal in size; but if their production subserves a definite and important function, we should expect that in some cases their formation would become a regular process, governed by definite laws. It is possible that the more symmetrical kinds of direct division are to be explained in this way, and such an explanation seems to apply well, as suggested on a preceding page, in the case of the scorpion's serosa. Division of the cell does not follow as a rule, and upon this fact Chun lays stress. But, so far as we know, there is nothing to exclude the *subsequent* occurrence of cell division, and it is even probable that cell division is induced by the presence of more than one nucleus. This I take to be the case in the scorpion's serosa, where I believe the division of the cell is due in part to the dicentricity set up in the cytoplasm by the division of the nucleus.

The study of nuclear division among the Protozoa seems likely to throw much light upon the relations of amitosis to mitosis, for there can be little doubt but that this group presents the most primitive types of nuclear division. So far as known, the very lowest forms of animal cells (*Amœbæ*) always divide by the direct method, as the study of *Amœba polypodia* by F. E. Schulze ('75), and of *Pelomyxa villosa*, *Amœba secunda*, and *A. proteus* by Gruber ('83 and '85), has shown. The division of the nucleus of *Amœba proteus* takes place by a sharp equatorial cleft, passing through the large, centrally placed nucleolus, and dividing that and the peripheral zone of chromatin into two exactly equal halves, which afterwards move apart. This is regarded by Gruber ('83, p. 385) as a simple type of karyokinesis, because an exact division of the chromatin is accomplished. No kinetic change of the chromatic substance is necessary to bring this about, hence none occurs. It seems to me that the absence of centrosomes and a spindle effectually separates this type of division from true karyokinesis, and until these are discovered, the nuclear division of *Amœba proteus* must be relegated to amitosis. The presence of so perfect a type of karyokinesis as that found in *Euglypha alveolata*, worked out so completely by Schewiakoff ('88), is strong evidence against the hypothesis that karyokinesis was gradually evolved from direct division. For here, among the lowest forms of animal life, we have nuclei dividing both by a simple constriction, and by the most highly developed kinetic changes.

Nuclear division among the Infusoria is of special interest, for we regularly find in the same individual nuclei very different in structure and function, — macro- and micronuclei. The former divide directly, the latter by karyokinesis. Apparent exceptions are seen in *Spirochona gemmipara*, where, according to R. Hertwig ('77) the macronucleus divides by karyokinesis; and in *Opalina ranarum*, studied most carefully by Pfitzner ('86^{b}). As only one kind of nucleus is found in Opalina, it is probable, as Bütschli suggests ('88, p. 1500), that these are of the micronuclear type, inasmuch as the division is in all essential respects like that of micronuclei, and in the resting state the nuclei bear no resemblance to macronuclei. The direct division of macronuclei is often accompanied by a longitudinal arrangement of the chromatic filaments, resembling that found in the scorpion's serosa (see Figs. 6, 7, 8). It seems to me that Carnoy is wrong in speaking of these longitudinal filaments as a "spindle," for it has never been shown that they converge to the poles of the nucleus, and frequently they can be resolved into granules, which is never the case with spindle fibres. Their resemblance to the spindle of karyokinesis is deceptive. From their behavior with stains, I regard them as consisting of chromatin, and Bütschli ('88, p. 1526) speaks of this stage of the macronucleus as the "Knäuelstadium," implying that the parallel filaments are chromatic threads.

Among the Vertebrates, amitosis is unusual, and where it exists karyokinesis is generally found to occur in cells of the same kind. It is almost confined to cells *which do not form fixed tissues*, as leucocytes of all kinds, and "giant cells," especially those of the red marrow. It also occurs in testicular cells of Vertebrates. In leucocytes, according to all observers, the nuclear division takes place by constriction, and is frequently accompanied by division of the cytoplasm (Ranvier, '75; Flemming, '82, p. 344; Arnold, '87). But, as the recent work of Flemming ('91) and others shows beyond a doubt, leucocytes also divide by karyokinesis. It is difficult to say whether there is more than a single kind of leucocyte, one dividing directly, the other indirectly, or whether cells of the same kind divide in two different ways. In case of giant cells, it has been shown by Arnold ('84), Denys ('86), Demarbaix ('89), and others, that division occurs both directly and by multiple karyokinesis. Both kinds of division are followed by division of the cytoplasm, leading to the formation of a brood of daughter cells within the mother cell.

After going over the literature of amitosis, taking especial note of the manner of its occurrence and distribution in the Animal Kingdom, I have become convinced that it is not derived from mitosis, and, on the other hand, is not the forerunner of the more complicated process. I consider it another type of division altogether, which, along with karyokinesis, has been transmitted from the simplest forms of life to the most highly organized. While apparently every kind of nucleus may, at some stage of its existence, divide by karyokinesis, many afterwards exchange this type of division for the simpler process. The special conditions which evoke the exchange are very imperfectly understood, and no hypothesis has yet been offered that will explain all the known instances. Some of the hypotheses that have been suggested I have already dwelt upon at length; others, as *scantiness* of chromatin, and even its *entire absence* in the nucleus (Löwit, '90), seem to me still more inadequate.

One fact in favor of the independence of the two types of division is the *sudden change from mitosis to amitosis, without any visible intermediate stages.* Phylogenetically, this is seen in the abrupt transition from the amitotic division of *Amœbæ* to the very perfect karyokinesis of the nearly related *Euglypha.* Ontogenetically, of course, the exchange is far more abrupt. In the conjugation of Infusoria, all divisions of the micronucleus are undoubtedly mitotic, while the *first* (after conjugation) and all subsequent divisions of the macronucleus, *itself formed from modified micronuclei*, are by direct division. Again, the amitosis of the blastodermic nuclei of *Blatta* (Wheeler, '89) is an abrupt change from the perfect mitosis of segmentation. Other instances are the sudden change from mitosis to amitosis in the layers of stratified epithelium, and in the generations of spermatic cells.

Another fact in favor of my view is the *almost universal distribution of amitosis, and its occurrence in many kinds of cells with widely different functions.* It seems more reasonable to suppose that a process so widely extended is *inherited*, and exists potentially in all cells, rather than to look upon it as independently assumed in a multitude of special cases. The latter supposition is opposed to all we know of the transmission of fundamental characters.

While it is evident that both mitosis and amitosis appeared at a very early period of organic life, it is impossible to say which appeared first. But, on *a priori* grounds, we may conclude that the simpler type preceded the more complex.

CAMBRIDGE, September 28, 1891.

It was not until this paper had gone to press that I had access to the recent communications on amitosis by Flemming ('91^a), Löwit ('91), Verson ('91), Frenzel ('91), and O. vom Rath ('91). In his review of recent work on cell division, Flemming says (p. 139): "Es ist also nicht nur als feststehend anzusehen, dass Amitose vorkommt, sondern auch, dass sie in normal lebenden Geweben vorkommt, und dass sie zur

Zellenvermehrung führen *kann.*" When, however, both mitosis and amitosis occur in the same tissue, he considers it probable that only the former is the *normal* method of regeneration and of growth.

The brief papers by Löwit, Verson, and Frenzel are replies to Ziegler's ('91) recent article on amitosis, and contain little that is new. Verson describes briefly the early stages in the spermatogenesis of the silkworm (*Bombyx mori*). He states that the spermatocytes originate from a single large nucleus ("Riesenkern"), which divides repeatedly and unequally by amitosis. The small daughter nuclei thus produced *divide by mitosis,* and at length form the spermatocytes. Frenzel adduces instances of amitosis in the intestinal epithelium of Crustacea and Insects which do not fall within Ziegler's generalizations.

Vom Rath's paper is a valuable contribution to our scanty knowledge of the occurrence of amitosis in spermatogenesis. He shows very conclusively that, in the testis of the crayfish, amitosis does not occur in the generations of sperm-forming cells, but only in abortive nuclei ("Randkerne"), which soon degenerate into an amorphous mass. If such a fate could be established for all amitotically dividing nuclei in the testes of animals, it would be much easier to form a logical estimate of amitosis.

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EXPLANATION OF FIGURES.

All figures are from drawings made with the aid of an Abbé camera.

PLATE I.

Fig. 1. Five cells of the serosa, two of them covered by the amnion, which is omitted from the rest of the figure for the sake of clearness. *am.*, amnion; *sr.*, serosa. × 150.

Fig. 2. Section through the embryonal membranes and ovarian capsule. The fibrous appearance of the ovarian capsule is due to the presence of muscle fibres and connective tissue. The boundary line between amnion and serosa is visible only in the vicinity of the amniotic nuclei. *e'th. fol.*, epithelium of ovarian capsule (when the plates were engraved I still took this to be the follicular epithelium, hence the error in the abbreviation); *nl. fol.*, nucleus of capsular epithelium; *nl. sr.*, nucleus of serosa; *nl. am.*, nucleus of amnion. × 630.

Figs. 3–15 are all from the *serosa.*

Fig. 3. Very small, binucleate cell. × 130.

Figs. 4–10. Nuclei at different stages of division. *vac.*, vacuole; *x*, new nuclear wall within the old one. × 550.

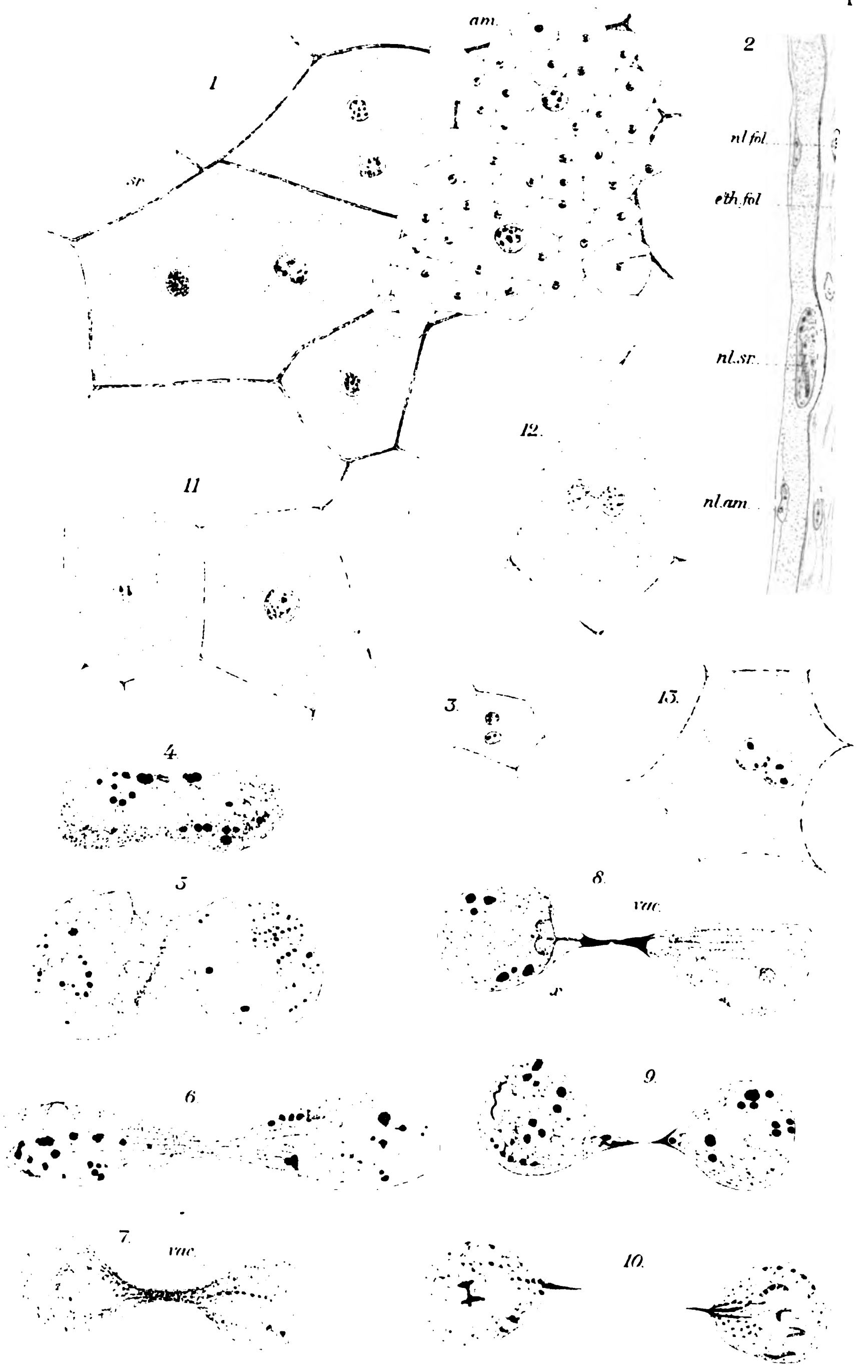
Fig. 11. Two cells produced by division of a binucleate cell. × 130.

Fig. 12. Cell from the serosa of a young embryo, with dividing nucleus; the axis of elongation corresponds with the *short* axis of the cell. × 130.

Fig. 13. Cell from serosa of a young embryo, with nucleus unequally divided and daughter nuclei eccentric in position. × 130.

JOHNSON NUCLEAR DIVISION

PL. I.



H. P. J. del.

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PLATE II.

Fig. 14. Piece of the serosa from an advanced embryo, with four adjacent trinucleate cells (1, 2, 3, 4); nuclei of cell *a* and the large cell farthest to left have undergone degeneration. × 90.

Fig. 15. Three cells of the serosa from an old embryo to show recession of daughter nuclei towards the ends of the cells. × 90.

Figs. 16–20 are from the *amnion*.

Figs. 16–19. Stages in the division of amniotic nuclei. In Figure 18 three stages are shown, *a*, *b*, *c*. × 800.

Fig. 20. Two amniotic cells, apparently formed by recent division. × 375.

Figs. 21–26 are from the *capsular epithelium*.

Figs. 21–23. Cells showing successive stages of nuclear division. × 800.

Figs. 24–26. Cells to show the degeneration of nuclei. In Figure 24 the nuclei are but slightly differentiated; in Figure 25 the pale nucleus has become much larger and very faint; in Figure 26 it has disappeared altogether. × 800.

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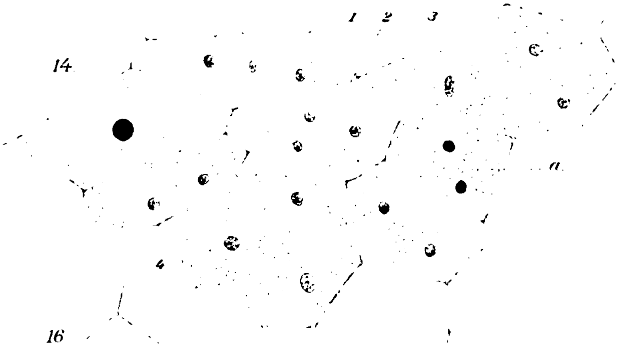

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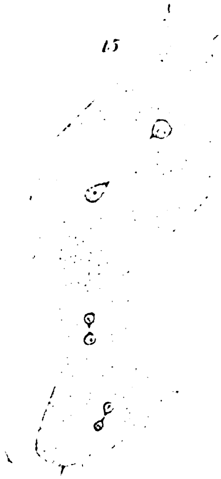

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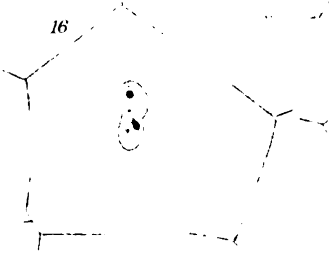

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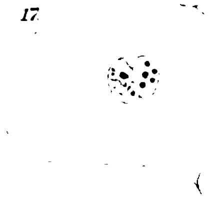

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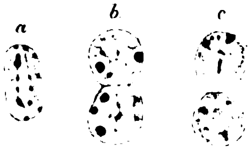

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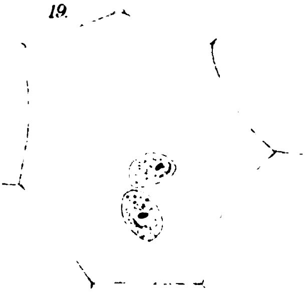

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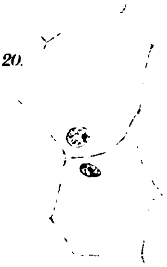

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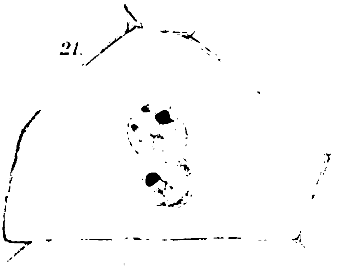

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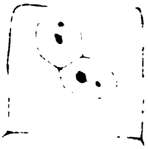

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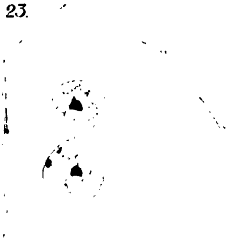

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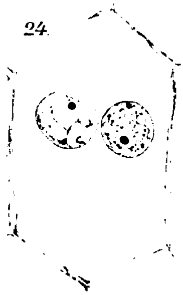

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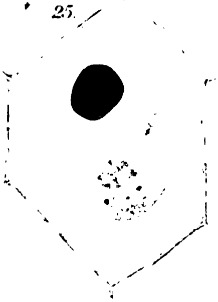

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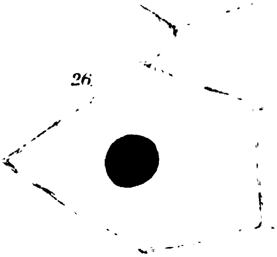

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PLATE III.

Figs. 27–34 are all from the *serosa*.

Fig. 27. A cell undergoing division by formation of a cell plate. The daughter nuclei are still united by a connecting thread. The dotted line on the left indicates the edge of the fragment of membrane in which this cell occurs. From the serosa of an advanced embryo. × 304.

Fig. 28. A cell divided by constriction, without the formation of a cell plate. The nuclei have undergone degeneration. From the serosa of an advanced embryo. × 150.

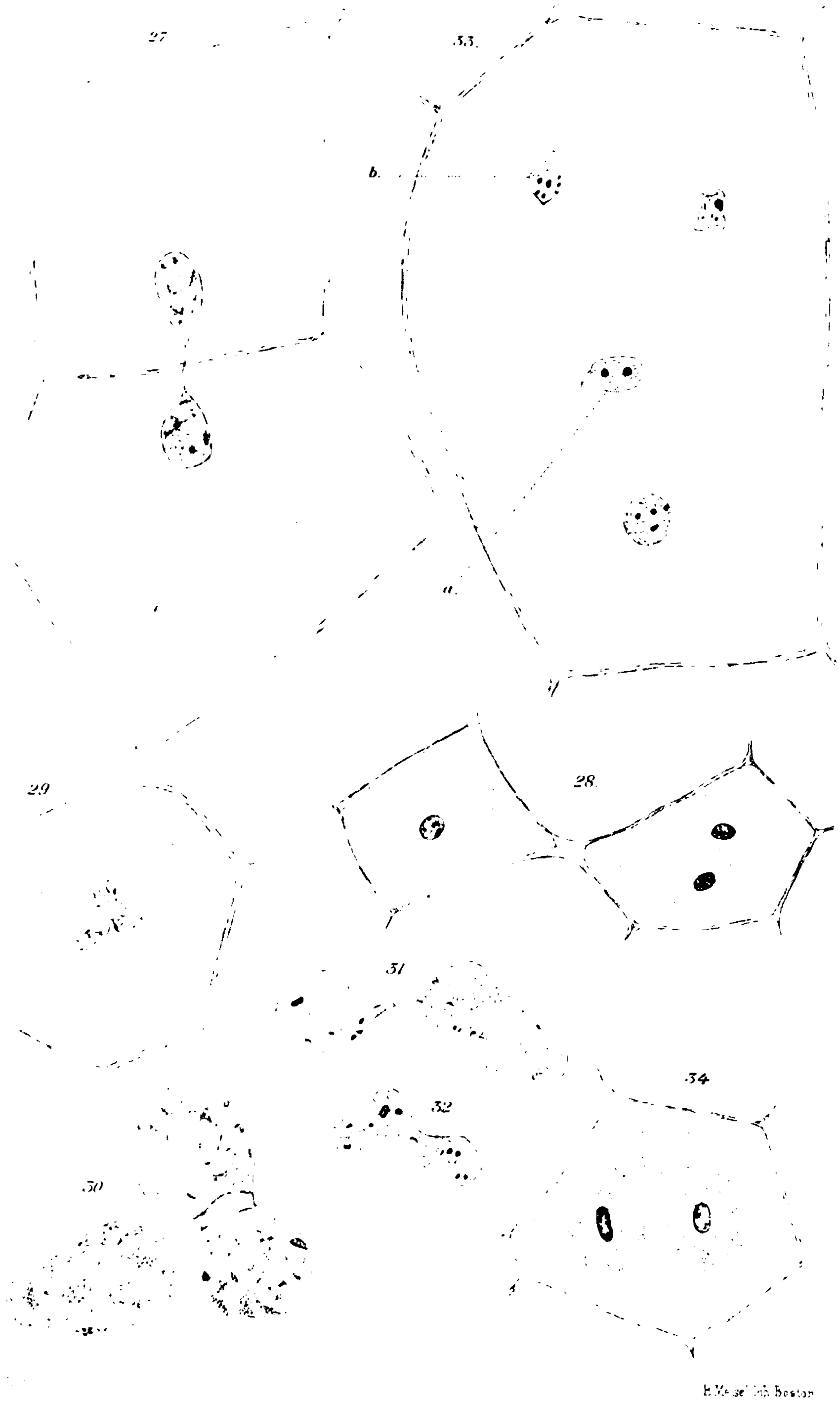
Fig. 29. A cell, the nucleus of which has undergone tripartite division. From an old serosa. × 150.

Fig. 30. Nucleus of the same, more highly magnified. The chromatin is grouped in granular masses. Two of the daughter nuclei are still united by strands of the nuclear membrane. × 630.

Figs. 31–32. Constricted nuclei from a young serosa. One of the daughter nuclei of each is larger than its mate, and has itself become elongated and constricted. × 304.

Fig. 33. Quadrinucleate cell. The upper of the two original nuclei has divided in a longitudinal, the lower in a transverse plane. Nucleus *a* still shows a remnant of the connecting thread, and nucleus *b* retains the conical form it had in division. Both nuclei have rotated 90° from the plane of elongation. × 304.

Fig. 34. Cell from the serosa of a far advanced embryo. The nuclei have undergone extreme degeneration. Each nucleus is surrounded by a bright ring, outside of which is a broad zone of a radiate structure, more stainable than the rest of the cytoplasm. × 150.



B. Meisel lith. Boston

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